ENVIRONMENTAL CORRELATES TO AMPHIBIAN AND REPTILE DIVERSITY IN COSTA RICA

A Thesis

by

DAVID EDELMAN LAURENCIO

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2007

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Lee A. Fitzgerald
Committee Members,	James R. Dixon
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ABSTRACT

Environmental Correlates to Amphibian and Reptile Diversity in Costa Rica.

(May 2007)

David Edelman Laurencio, B.S., Texas A&M University

Chair of Advisory Committee: Dr. Lee A. Fitzgerald

The study of species diversity patterns and their causes remains a central theme of ecology. Work conducted over the last few decades has shown that both historical and ecological factors are important in determining species diversity patterns. Additionally, different causal mechanisms are important at different spatial and temporal scales. At the regional scale, species diversity patterns can best be studied in terms of three diversity components (alpha, beta and gamma). This study used the amphibians and reptiles of Costa Rica to examine these species diversity components at the regional scale. To accomplish this, existing species lists were compiled from the literature. Additionally, three herpetofaunal surveys were conducted at under surveyed sites to fill knowledge gaps.

A survey of Parque Nacional Carara, a transitional zone site on Costa Rica's central Pacific coast, gave evidence of a rich herpetofauna, containing species from both the dry tropical forest to the north and the wet lowland forest to the south. Survey results show that Carara's herpetofaunal assemblage is more similar to that of the wet forest than the dry forest, and suggest many species from both assemblages reach their range limit at or near the park. Surveys of four sites in the eastern Área de Conservación Guanacaste showed rich herpetofaunal diversity and validated the newly purchased

Rincón Rainforest as an important conservation area. A survey of Reserva Natural Absoluta Cabo Blanco provided a preliminary list of amphibian and reptile species of the lower Nicoya Peninsula and highlighted the importance of Laguna Balsitas to the local amphibian fauna. A comparison of amphibian and reptile alpha diversity among 17 sites throughout Costa Rica showed highest alpha amphibian diversity in the lowland rainforests of the Pacific versant and highest reptile alpha diversity in lowland rainforests of the Atlantic versant. An analysis of beta diversity produced dendrograms showing sites within lowland ecoregions being most similar. A Canonical Correspondence Analysis (CCA) of environmental variables showed two climate gradients, an elevation/temperature gradient and a sun/rain gradient, to be important in determining species diversity patterns for both amphibians and reptiles in Costa Rica.

Para mis padres

Para mis padrinos

Para Laura

Ustedes me han dado las enseñanzas más importantes de la vida.

Tienen mis gracias.

ACKNOWLEDGMENTS

I could not have, nor did I want to, set out on the journey that was the completion of this thesis on my own. A myriad of people gave of their time and effort in order to make this work possible. I have gained much, not only academically, but also professionally and personally by being surrounded by excellence. I have learned much from all of you, and I am deeply grateful for each of you and for your help. If you were a part of this project and do not see your name, I apologize. Know that your help was appreciated and the omission of your name was due only to an oversight by me at the time of writing this.

Let me begin by thanking my committee members for their support and guidance. Your insights, ideas and comments greatly improved my thesis.

Special thanks to Dr. Lee A Fitzgerald both for taking a chance on me, and for your continued belief in me. Lee, you have given me a chance at a life I could only have dreamed of. I am forever indebted to you, and I hope I will make you proud.

Special thanks also to Dr. James R. Dixon, for all of his help and instruction over the years, both in Texas and in Costa Rica. I feel especially fortunate to have had you (and Mary) join us in on our field expeditions to Costa Rica. Your experience, expertise and guidance went a long way towards making those trips a success. They would not have been the same without you.

I would also like to extend special thanks to John H. Malone and Toby J. Hibbitts. Everything I know about herping I learned from the two of you. I can say I

have learned from the best. Thank you for all that you have taught me, for answering all of my questions (some of them repeatedly), and for transferring your love and passion for all things herp to me. I am lucky to have found such able naturalists and herpetologists to learn from and blessed to have found such good people to call friends.

Field portions of this project were completed with the help of a small army. One could say we were a group of people who independently love to study herpetology, a Herpetological Independent Study Group if you will. For their help in the field I would like to thank Dr. J. R. Dixon, Mrs. Mary Dixon, Rachel Gallagher, Dr. Toby J. Hibbitts, Robert Hibbitts, David LaFever, Joel Johnston, Juan Laurencio (my dad), Laura Laurencio, Jacob Malcolm, Joe McKinney, Kristen Millenbach, Rebecca Ryberg, Wade Ryberg, Julie Traweek, Toby Ware and Thad (TJ) Williams. Additionally, thank you Roy Salas and family as well as all Junior HISG members. A thank you is also in order for the park system volunteers, for not only helping us with our field work, but also for giving of their time to help support Costa Rica's national parks system.

Thank you to the staff of the Ministerio del Ambiente y Energía, both at the ventanilla única, and at Parque Nacional Carara, Área de Conservación Guanacaste, and Reserva Natural Absoluta Cabo Blanco. I thank them for their logistic support, for permission to work in such beautiful areas, as well as for sharing their living space, time and food with us while we were in the parks. Most importantly, I thank them for imparting us with their knowledge. We all learned much from each person we came across. Additionally, thanks to Dr. Dan Janzen and Dr. Dan Brooks for their assistance in the ACG.

For their continual help at the UCR in Costa Rica, I thank Federico Bolaños, Gerardo (Cachí) Chaves and Alejandro Solórzano. Thanks also to Dr. Jay M. Savage for his help in identifying specimens as well as for his life's work in Costa Rica and serving as an inspiration.

Thank you to the members of the Fitzgerald Herpetology Lab, both past and present. At some point I think I have pestered each of you to discuss science, herp, bounce ideas off of, or to have you read, edit or comment on a paper or talk. I have enjoyed our time together and your comments, thoughts and ideas have helped to improve my thinking and my work. Special thanks to the current lab members who read over and helped improve drafts of this thesis and its corresponding manuscripts.

Thank you to all the students, staff and faculty of the Department of Wildlife and Fisheries Sciences that have helped me over the years, especially to Vicki Buckbee, Janice Crenshaw, Shirley Konecny, Diann Radke, Melissa Rubio and Dr. Markus Peterson. Thanks to David Hoeinghaus and Steven Zeug for their help with ordination and CONOCO.

Thank you to Freebirds for feeding me well. May you stay non-corporate.

I extend special thanks to my mother who has not only been the driving force behind my education, but who also has been an integral part of all of our Costa Rican field expeditions. She has done more than can be written here, including disrupting her life to open her house to all of our field crews, feeding us, providing logistic support and even helping me acquire permits. Without her help, our field exploits would have been immeasurably more difficult.

Last, I would like to thank my wife Laura, whom I did not invite on our first field trip. Thank you for allowing me to follow a dream. Thank you more for becoming a part of it. Without your continued support and sacrifice, I would not be writing these words today. I am blessed to have you.

The field work for this thesis was conducted under the following MINAE permits: Resolución No. 237-97-OFAU, Resolución No. 237-98-OFAU, Resolución No. 019-2000-OFAU, Resolución No. 342-2000-OFAU, Resolución No. 217-2001-OFAU, Resolución No. 168-2003-OFAU and under AUP No. 2003-230. Funding for field portions of this study was provided in part by the East Texas Herpetological Society, The Explorer's Club, Durman Esquivel S. A., and by a generous donation from the Ryberg family.

NOMENCLATURE

ACG	Área de Conservación Guanacaste
ACOPAC	Área de Conservación Pacífico Central
BC	Bajo Carara
BFS	Bijagual Field Station
CCA	Canonical Correspondence Analysis
CM	Cerro de la Muerte
CT	Highland-Cordillera de Talamanca
EBC	Estación Biológica Cacao
EBSM	Estación Biológica San Miguel
EC	Estación Caribe
ECB	Estación Cabuya
HQ	Headquarters
JSI	Jaccard's Similarity Index
LA	Lowland Atlantic Forest
LP	Lowland Pacific Forest
LB	Laguna Balsitas
MA	Middle American Element
ME	Mid-elevation Sites
MINAE	Ministerio del Ambiente y Energía
NW	Lowland-Pacific Northwest

ON	Old Northern Element
PET	Potential Evapotranspiration
PNC	Parque Nacional Carara
PNSR	Parque Nacional Santa Rosa
RCC	Rincón-Caribe Corridor
RNACB	Reserva Natural Absoluta Cabo Blanco
RR	Rincón Rainforest
SA	South American Element
SCC	Upland/Highland Montane Slopes and Cordillera Central
SG	Estación San Gerardo
SINAC	Sistema Nacional de Áreas de Conservación
SW	Lowland-Southwest
TCWC	Texas Cooperative Wildlife Collection
TDF	Tropical Dry Forest
UCR	Universidad de Costa Rica
UPGMA	Unweighted Pair Group Method Using Arithmetic Averages
USA	United States of America
VES	Visual Encounter Survey

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CHAPTER I

INTRODUCTION

Determining patterns of species distributions and the factors influencing these patterns has been a focus of ecologists and biogegraphers for several decades. Knowledge of species diversity is fundamental to understanding basic patterns of community ecology (Schiebe, 1987), and understanding these patterns and their causes is paramount to any biogeographic study or conservation effort. This understanding becomes increasingly important in light of current rates of habitat destruction and fragmentation, which have created the current biodiversity 'crisis' (Soulé, 1986; Raven & Wilson 1992). Patterns of species diversity are complex phenomena and despite several decades of research, many questions remain (Owen, 1989). However, trends seen in studies of species diversity and their correlates suggest that these patterns have explanations (Schall & Pianka, 1977).

Costa Rica provides an excellent model for studying species diversity and its correlates. A small country (50,900 km²), approximately the size of West Virginia, Costa Rica contains close to 4% of the earth's total biodiversity (Vargas Ulate, 1992). This diversity is reflected in its herpetofauna, which consists of 174 amphibian and 222 reptile species (Leenders, 2001; Savage, 2002). These species are distributed among a varied landscape which includes many climatic regimes, life zones, and elevations, which facilitate the study of factors correlated to diversity. Furthermore, the country has

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This thesis follows the style and format of *Journal of Biogeography*.

protected approximately twenty five percent of its land and has for many years encouraged biological study. This has led to a thorough documentation of the country's herpetofauna.

This study will investigate patterns of herpetofaunal species diversity in Costa Rica, and elucidate factors influencing these patterns. This will be accomplished by comparing herpetofaunal assemblages at 17 sites from throughout the country. Furthermore, this study will extend the knowledge of species richness at a local scale through the completion of three baseline herpetofaunal inventories. This is an important benefit to both the national parks where the inventories are conducted, and to scientific understanding because of the need for such inventories at neotropical sites to facilitate comparative studies (da Silva & Sites, 1995). The objectives of this study are the following:

1. The description of the amphibian and reptile fauna of Parque Nacional Carara, Costa Rica
2. The description of the amphibian and reptile fauna of the Eastern Guanacaste Conservation Area, Costa Rica
3. The description of the amphibian and reptile fauna of Reserva Natural Absoluta Cabo Blanco, Costa Rica
4. The description of geographical patterns of species richness of Costa Rican amphibians and reptiles in terms of diversity components
5. The elucidation of abiotic factors influencing amphibian and reptiles species diversity patterns in Costa Rica

CHAPTER II

STATEMENT OF KNOWLEDGE

Species Richness Patterns

Ecologists have studied geographic patterns of species richness for several decades, and a myriad of hypotheses have been formulated to account for geographic variations in species richness (Ricklefs & Schluter, 1993a; Rosenzwieg, 1995; Brown & Lomolino, 1998). Early work focused on ecological aspects related to these patterns such as habitat structure and latitudinal gradients of diversity (MacArthur & MacArthur, 1961; Pianka, 1966a; Pianka, 1966b; Terbourgh, 1973). Recent work has emphasized the effects of spatial scale and complexity (Mökkönen, 1994; Bohning-Gaese, 1997; Davidowitz & Rozensweig, 1998; Stillman & Brown, 1998) as well as the importance of historical factors (Brooks & McLennan, 1993; Cadle & Greene, 1993; Ricklefs & Schluter, 1993*a*, *b*, *c*). As Cody (2001) states, there are "clearly a multitude of factors, operating on a wide range of temporal and spatial scales", that are responsible for the maintenance of species diversity patterns. Currie (1991) summarized some of these factors. They include the following: climate, climatic variability, habitat heterogeneity, history, energy, competition, predation, and disturbance. These factors are not mutually exclusive and work together to determine diversity patterns, however, each factor's importance is dependent on the scale of the study.

Scale

Ecologists have traditionally worked at local scales and have looked for biotic explanations (competition, predation, etc.) for the species diversity seen, while biogeographers have focused on continental and macro scales, looking for geographical and historical explanations for diversity patterns. Generally, it is believed that while all factors contribute to the overall diversity of a given area, different factors play greater or lesser roles depending on the scale being investigated. At local scales, biotic interactions and the micro habitat structure play the most important role at structuring the community, while at macro scales, regional and historical factors are most important. Because of this, the choice of scale of the units within the study area is a critical decision (Birks, 1987). This study will be conducted at the regional scale.

Diversity Components

At regional scales, patterns of species diversity can be best understood by breaking them down into three diversity components (Cody, 1983; Cody, 1986; Cody, 1993; Cody, 2001). This enables better understanding of observed patterns, and elucidates factors influencing regional diversity. This study follows Whittaker's (1972) diversity component definitions. Alpha (α) diversity is defined as the number of species within a habitat type at a particular locality or site. Alpha diversity is equivalent to a local site's species richness. Confusion exists as to the use of this term. The terms species richness, species diversity and species density have been defined differently by different authors. Generally, species richness is simply the number of species sampled at a given site. Species diversity is frequently defined as species richness, but more

commonly it is represented by an index that accounts for both number of species and the abundance of each. Species density is a term used for the number of species sampled in a given area (e.g. per unit area). This study will use species richness as defined above, the number of species sampled at a given site, as the measure of α-diversity.

Beta (β) diversity is defined as the difference in species composition between two sites. This difference may be due to a turnover of species between habitat types or the replacement of species among the same habitat type. While β-diversity can be as important as α-diversity at determining regional diversity (Harrison *et al.,* 1992), β-diversity has received far less study. Beta diversity is usually presented in terms of a similarity or dis-similarity index based on the number of species shared between the sites and the total number present in each. Wilson & Shmida (1984) explain the importance of β-diversity measures: 1) they indicate the degree to which habitats have been partitioned by species, 2) they can be used to compare the habitat diversity of different sites, 3) used with alpha diversity, they can measure the overall diversity of a region.

Gamma (γ) diversity is the overall diversity across a landscape or region. It consists of both the region's alpha and beta diversity. Different authors have provided various means of calculating gamma diversity. Traditionally it was viewed as the multiplicative sum of alpha and beta (Whittaker, 1972). Others argue that gamma diversity is simply the sum of alpha and beta diversity (Loreau, 2000).

Herpetofaunal Diversity

Biogeographical studies on herpetofaunal patterns of species diversity have focused primarily on describing species richness on continental (Kiester, 1971; Currie,

1991) or regional scales (Poynton & Bass, 1970; Busak & Jaksić, 1982; Owen, 1989; Crowe, 1990; Real *et al.,* 1993), although some authors have focused on local scales. Correlates to changes in species diversity have been studied on regional (Duellman, 1966; Rogers, 1976; Scheibe, 1987; Owens, 1989; Crowe, 1990) and continental scales (Currie, 1991). Results from these studies varied, but generally, factors found to be correlated with species diversity included temperature (Duellman, 1966; Rogers, 1976; Scheibe, 1987; Crowe, 1990), precipitation (Duellman, 1966; Rogers, 1976; Scheibe, 1987; Owens, 1989; Crowe, 1990), topography (Rogers, 1976; Owens, 1989; Crowe, 1990) and Potential Evapotranspiration (PET) (Currie, 1991).

In Costa Rica, much of the work on species diversity has been in the form of biogeographical studies focused on the formation, history of, maintenance and environmental correlates to the Central American herpetofauna (Duellman, 1966; Savage, 1966; Savage, 1982; Savage, 2002; Stuart, 1966; Vanzolini & Heyer, 1985; Campbell, 1998). However, some studies have focused on alpha diversity of specific areas. Donnelly (1994) and Guyer (1994) presented species lists from the amphibians and reptiles of La Selva and compared these to other neotropical sites. Sasa & Solórzano (1995) compiled a species list of amphibians and reptiles of Parque Nacional Santa Rosa and comment on the herpetofauna of xeric areas. Bolaños & Ehmcke (1996) formulated a species list of the San Ramon area and compared the site to three others within Costa Rica. Burger (2001) provided a species list for the amphibians and reptiles of the Tortuguero area.

Transition Zones

In areas where large vegetative zones collide, a transition zone can exist that both physically and biologically fits between the two neighboring habitats (Williams, 1996; Brown & Lomolino, 1998). This zone may contain species from the two adjoining habitats in a unique combination, and if the transition zone contains endemics, it can even have higher species richness than that of the two major habitats (Ramanamanjato *et al.,* 2002). From a conservation standpoint, these transition areas can be important for several reasons (Ramanamanjato *et al.,* 2002). If the area contains a high percentage of the species richness of each of the adjoining major habitat types, protecting it would maximize the protection of total species number. Furthermore, the area could serve as a connection between the two major habitat sites, contain species of special concern or it could house a unique blend of species that would warrant conservation protection in their own right. For those reasons, exploring biotic transition zones is an essential part of studying the processes that govern the distribution and diversity of organisms (Williams, 1996).

One such zone occurs along the central Pacific coast of Costa Rica. It lies between the country's dry forest in the northwest and very wet rainforest in the southwest and serves as transition zone between these two distinct habitats and their corresponding herpetofaunal assemblages. The area is of added interest because little herpetological work has been conducted along the central Pacific coast. Indeed, prior to this study, its one major national park, Parque Nacional Carara, had not been

inventoried. Conducting an inventory in this area helps fill a knowledge gap while providing diversity data that will be used for this and other comparative studies.

CHAPTER III

THE AMPHIBIANS AND REPTILES OF PARQUE NACIONAL CARARA, COSTA RICA

Synopsis

Parque Nacional Carara is located midway along the Pacific versant of Costa Rica in the transition zone between dry tropical forest to the north and wet tropical forest to the south. This study documents patterns of biodiversity among three sites within Parque Nacional Carara as well as compares the park's overall herpetofaunal community to the those found in the dry tropical forest to the north and to the tropical rainforest to the south. Forty-one amphibian and 65 reptile species were documented for Carara. Within the study site, the lowland locality contained the highest species richness. Both dry and wet forest species were found in the park, although there was a closer resemblance to the wet forest assemblage for both amphibians and reptiles. An analysis of the fauna's generic origins showed that the park contained a transitional assemblage corresponding to neither the southwestern nor the northwestern faunal area as defined by Savage (2002). Because Carara is the only large protected area in this region, its importance to the preservation of this unique faunal assemblage is paramount.

Introduction

The herpetofauna of Costa Rica is one of the best known and most studied in the Neotropics with over 400 documented species of amphibians and reptiles (Savage,

2002). This body of knowledge has been built upon herpetofaunal surveys that documented species occurrence in a wide variety of habitats and geographic localities, including Pacific and Caribbean lowland rainforests (Donnelly, 1994; Guyer, 1994; McDairmid & Savage, 2005), tropical dry forests (Sasa & Solórzano, 1995), and cloud forests (Hayes *et al.,* 1989). However, the herpetofauna of Costa Rica's Central Pacific coast remains virtually undocumented. This area is of particular interest to biodiversity scientists as it is a transition zone between the tropical dry forest in the Northwest and the lowland rainforest of the Osa Peninsula to the Southwest.

Transitional zones occur at the boundary of two discrete biomes or habitat types and can be narrow and sudden, or more gradual across the landscape (Williams, 1996). Often, these areas have physical and climatic attributes intermediate to the adjacent habitats (Brown & Lomolino, 1998). As a result, assemblages in transitional zones are often a blend of those found in the adjacent areas (Brown & Lomolino, 1998). However, if the transition zone also contains endemic species, its species richness may surpass that of the adjacent areas (Ramanamanjato, 2002). Additionally, these zones can be important centers of speciation and contribute to creation and maintenance of biodiversity in tropical forests. (Smith *et al.,* 1997). Transition zones thus have high conservation value, both in their own right and as connections between ecosystems (Ramanamanjato, 2002). An increased understanding of the patterns and processes that form transition zones is important to the explanation of local and regional diversity patterns (Gosz, 1992).

Parque Nacional Carara (PNC) stands as the largest tract of forest and the only significant protected area within the Central Pacific transitional zone. It is located almost equidistant from Parque Nacional Santa Rosa (PNSR), a typical tropical dry forest site to the north, and Rincón de Osa, a lowland wet rainforest site to the south. A comprehensive list of the herpetofauna of PNC will serve to document the species assemblage found in a central pacific transitional zone site and help elucidate the relationship of the local herpetofauna to that of the adjacent forests types. The objectives of the present study were to 1) present a list of the amphibians and reptiles found in PNC based on our surveys using multiple methods, 2) compare herpetofaunal diversity among three sites surveyed within PNC, and 3) compare the herpetofauna of PNC to that of the tropical dry forests to the north and lowland wet forests to the south in order to examine patterns of diversity in the Central Pacific transition zone.

It is expected that amphibian and reptile species assemblages at Carara will contain a mixture of dry and wet forest species found in adjacent habitats and as such, an analysis of its composition will provide insight as to the pattern of species turnover along the Central Pacific coast transition zone. Additionally, the Sistema Nacional de Áreas de Conservación (SINAC) will incorporate information on amphibians and reptiles of PNC into their management and outreach programs.

Methods

Study Site

Parque Nacional Carara (9° 45’ 22”N, 84° 36’ 27”W), is a 5200 ha natural area 40 km southwest of Orotina along Costa Rica’s central pacific coast. Lying in both Puntarenas

and San José provinces, PNC is bordered to the north by the Tárcoles River and to the west by the Costanera Sur highway (Hwy. 34, Fig. 1). Parque Nacional Carara is a forested island surrounded by a matrix of farmland and pasture. Carara is 95% forested and contains several habitat types including: swamps, oxbows, and primary, gallery and secondary forests (Boza, 1984). The majority of the park consists of primary forests and it is characterized by trees and other vegetation representative of both the tropical dry forest and lowland wet forest (Vargas Ulate, 1992). According to Tosi's (1969) habitat map, PNC contains tropical moist forest, tropical wet forest, and tropical wet forest premontane belt transition. Elevation within the park ranges from 30 to 636 m. Mean precipitation generally varies between 2000 and 3000 mm rainfall yearly with distinct wet (May – November) and dry (December – April) seasons (Boza, 1984; Barrantes, 1985). The annual mean temperature is 27.8° C (Vargas Ulate, 1992).

We conducted surveys in three sectors of the park: the lowland area, which included the park's headquarters and visitor center (abbreviated HQ), the area around the Bijagual Field Station (BFS), and the Bajo Carara region (BC) (Fig. 1). The lowland area included all public trails, the seasonally flooded forest of the Tárcoles floodplain, as well as an oxbow lagoon. This area contained several streams, the most important being Quebrada Bonita and Quebrada Pizote. The BFS area had the highest elevation (633 m) of the three study sectors, and was composed of a narrow strip of forest surrounded by farmland and pasture with one stream of importance, Quebrada Máquina. The BC guardhouse is located on the eastern edge of the park next to the Río Carara between a mosaic of cultivated lands outside the park's boundaries and primary and gallery forest

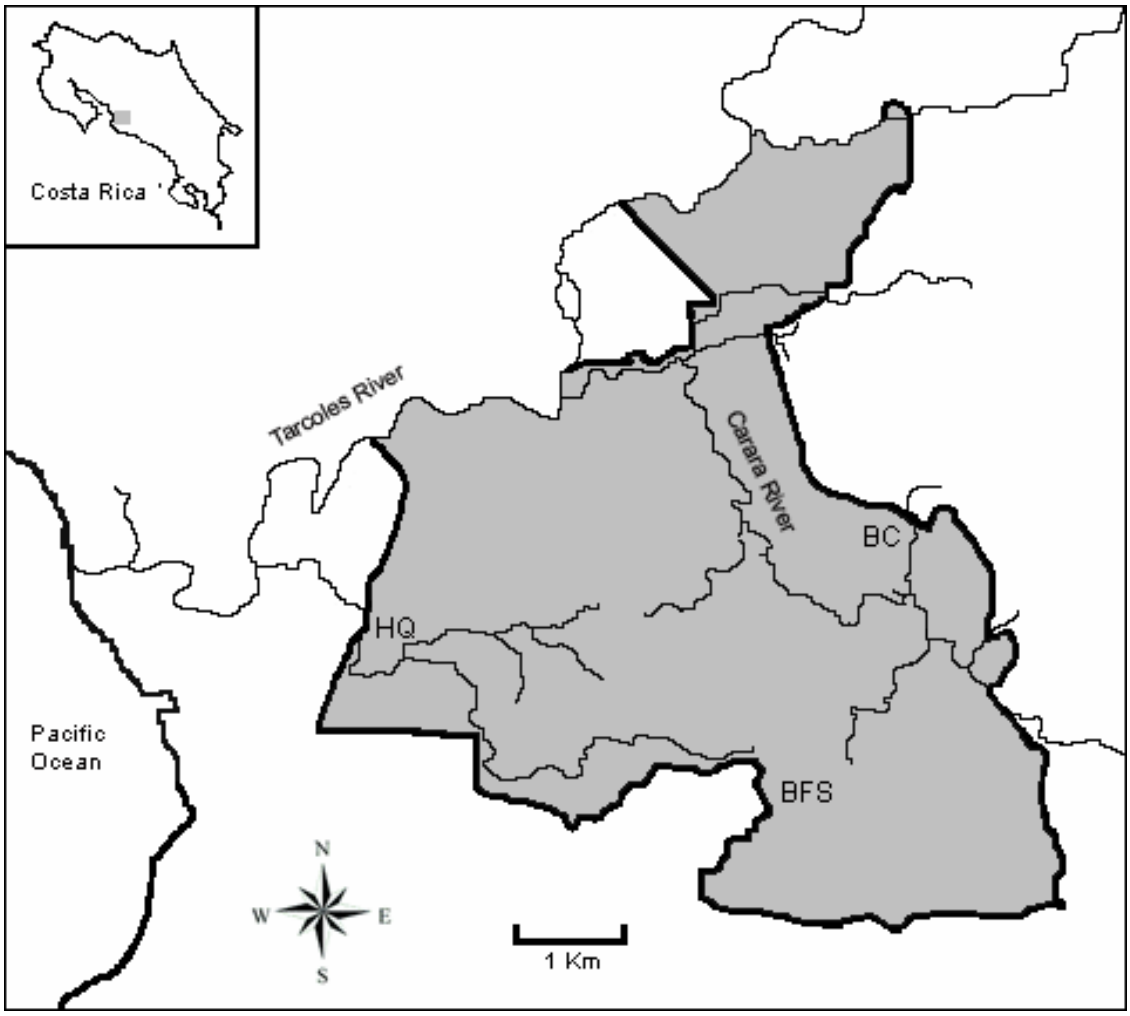

Figure 1 Map of Parque Nacional Carara, Costa Rica. Three surveyed sites are labeled: HQ – Headquarters, BFS – Bijagual Field Station, BC – Bajo Carara.

within the park. The dominant feature of this mid elevation (330 m) site was the river and its associated gallery forest.

Sampling

Sampling took place in both the rainy and dry seasons during 1998 – 2001. Primary collecting methods were diurnal and nocturnal visual encounter surveys (VES) (Crump & Scott, 1994), and drift fence arrays with pitfall and funnel traps (Corn, 1994). Five drift fence arrays were erected in the lowland and Bijagual regions (Fig. 1) using a 'Y' configuration (Corn, 1994) with 15 m drift fences constructed from aluminum flashing or polystyrene sheeting (Malone & Laurencio, 2004). Pitfall traps consisted of 20 L buckets buried at the end of each fence and in the center of the array. Two cylindrical 22.9 cm x 44.5 cm Gee Minnow Traps were placed on each drift fence, one on either side. Five drift fence arrays were erected in the lowland region (HQ) and five near the BFS (Fig. 1). Specimens were also collected via road cruising and opportunistically. Voucher specimens for each species were deposited at the Museum of Zoology of the University of Costa Rica (UCR) and the Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University. Tissue samples from voucher specimens were deposited in the frozen tissue collection at Texas State University. These survey data were supplemented with existing specimen records from the UCR as well as photographic evidence collected by Mr. Jim Kavney and verified by Alejandro Solórzano.

Faunal Comparisons

Qualitative estimates of species abundance (Tables 1 and 2) followed criteria used by Rand & Myers (1990). Alpha and beta diversity values were computed to compare faunal composition for the three within-park sites as well as compare the overall faunal composition of PNC to published species lists from a representative tropical dry forest site, Parque Nacional Santa Rosa (Sasa & Solórzano, 1995) and a tropical (lowland) wet forest site, Rincón de Osa (McDiarmid & Savage, 2005). Alpha diversity was defined as local species richness and beta diversity is defined as the difference in species between sites (Whittaker, 1972). Beta diversity was calculated using Jaccard's Similarity Index (Krebs, 1989), and a cluster analysis was performed on similarity values with the unweighted pair group method using arithmetic averages (UPGMA) algorithm (Sneath & Sokal, 1973).

Results

This study documented 41 amphibian and 63 reptile species for PNC, including one caecilian, three salamanders, 37 anurans, one crocodilian, two turtles, 24 lizards and 36 snakes (Tables 1 and 2). Most species were not common and were classified as rare or infrequent based on the scheme of Rand & Myers, (1990). The most common amphibian species were: *Dendrobates auratus*, *Smilisca phaeota* and *Bufo marinus*. Reptile species considered common were: *Ctenosaura similis*, *Ameiva leptophrys*, and *Norops cupreus*.

A total of two caecilians, 59 frogs, 112 lizards and 13 snakes were captured in drift-fence arrays over 2487 trap-nights. Four species were documented based solely on

Table 1 Relative abundance of amphibian species found in Parque Nacional Carara, Costa Rica. Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen.

Taxon	Abundance		
	HQ	Bijagual	Bajo Carara
GYMNOPHIONA (1 species)			
Caecilidae (1)			
Dermophis parviceps		R	
CAUDATA (3 species)			
Plethodontidae (3)			
Bolitoglossa lignicolor			R
Oedipina alleni		R	
Oedipina pacificensis		R	
ANURA (37 species)			
Microhylidae (1)			
Hypopachus variolosus	R		
Leptodactylidae (13)			
Eleutherodactylus cerasinus		R	R
Eleutherodactylus crassidigitus	R	R	
Eleutherodactylus diastema		I	R
Eleutherodactylus fitzingeri	C	C	U
Eleutherodactylus ranoides		R	R
Eleutherodactylus ridens		R	R
Eleutherodactylus rugosus	U		
Eleutherodactylus stejnegerianus	C	I	R
Leptodactylus bolivianus	R	R	
Leptodactylus labialis	R	I	
Leptodactylus melanonotus	I		
Leptodactylus pentadactylus	I	I	
Leptodactylus poecilochilus	U		
Bufonidae (4)			
Bufo coccifer	I	I	
Bufo haematiticus			R
Bufo marinus	C	C	I
Bufo aucoinea	R	U	R
Hylidae (11)			
Agalychnis callidryas	U	I	I
Hyla ebraccata	U		
Hyla microcephala	U		
Hyla rosenbergi	I	R	I
Phrynohyas venulosa	R		

Table 1 continued

Taxon	Abundance		
	HQ	**Bijagual**	**Bajo Carara**
Scinax boulengeri	R		
Scinax elaeochroa	R		
Smilisca baudinii	R		
Smilisca phaeota	C	C	C
Smilisca sila		R	U
Smilisca sordida	C	C	U
Dendrobatidae (1)			
Dendrobates auratus	C		
Centrolenidae (6)			
Centrolene prosoblepon		R	R
Cochranella albomaculata		R	R
Cochranella granulosa			R
Hyalinobatrachium colymbiphyllum	I		
Hyalinobatrachium fleischmanni		I	R
Hyalinobatrachium valerioi	I		R
Ranidae (1)			
Rana forreri	R	R	

Table 2 Relative abundance of reptile species found in Parque Nacional Carara, Costa Rica. Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen.

Taxon	Abundance		
	HQ	Bijagual	Bajo Carara
CROCODYLIA (1 species)			
Crocodylidae (1)			
Crocodylus acutus	C (Rio Tárcoles)		
TESTUDINATA (2 species)			
Emydidae (1)			
Rhinoclemmys pulcherrima	R		
Kinosternidae (1)			
Kinosternon scorpioides	I		
SAURIA (26 species)			
Gekkonidae (7)			
Coleonyx mitratus	I		
Gonatodes albogularis	C		R
Hemidactylus frenatus	U (Buildings)		
Hemidactylus garnoti	U (Buildings)		
Lepidoblepharis xanthastigma		R	R
Sphaerodactylus graptolaemus	R	R	
Thecadactylus rapicaudus	R		R
Corytophanidae (2)			
Basiliscus basiliscus	U	I	R
Corytophanes cristatus	I	I	R
Iguanidae (2)			
Ctenosaura similis	C		
Iguana iguana	I		
Polychrotidae (8)			
Norops biporcatus	R	R	R
Norops carpenteri	R		
Norops capito		R	
Norops cupreus	C	U	R
Norops limifrons		R	R
Norops oxylophus		R	R
Norops polylepis	C	R	R
Polychrus gutturosus	R		

Table 2 continued

Taxon	Abundance		
	HQ	Bijagual	Bajo Carara
Teiidae (4)			
Ameiva leptophrys	C		R
Ameiva quadrilineata	R		R
Cnemidophorus deppii	R		
Leposoma southi	R	R	U
Scincidae (2)			
Mabuya unimarginata	R		
Sphenomorphus cherriei	R	R	R
Xantusiidae (1)			
Lepidophyma reticulatum	R		
SERPENTES (36 species)			
Boidae (1)			
Boa constrictor	R		
Colubridae (31)			
Coniophanes fissidens	R	R	
Dendrophidion percarinatum	R	R	
Dendrophidion vinitor	R	R	
Drymobius margaritiferus	R		
Enulius sclateri		R	R
Geophis hoffmanni	R		R
Hydromorphus concolor			R
Imantodes cenchoa	I		
Imantodes gemnistratus	R	R	R
Imantodes inornatus	R		
Lampropeltis triangulum	R		
Leptodeira annulata	R		
Leptodeira septentrionalis	U	I	R
Leptophis ahaetulla	R		R
Leptophis nebulosus	?*		
Masticophis mentovarius	R		
Mastigodryas melanolomus	R	R	
Ninia maculata	R	R	R
Oxybelis aeneus	R	R	R
Oxyrhopus petola	R		
Pseustes poecilinotus	R		
Rhadinaea decorata	R	R	R
Sibon anthracops	R**		
Sibon dimidiatus	R		

Table 2 continued

Taxon	Abundance		
	HQ	Bijagual	Bajo Carara
Sibon nebulatus	I	R	
Spilotes pullatus	R**		
Tantilla armillata	R		
Tantilla ruficeps			R
Tripanurgos compressus		R	R
Urotheca decipiens		R	
Urotheca fulviceps		R	
Elapidae (2)			
Micrurus alleni	R	R	R
Micrurus nigrocinctus	R		
Viperidae (2)			
Bothriechis schlegelii	R	R	
Bothrops asper	C	I	U

* Voucher for this species occurs at UCR
** Identified from photo.

drift-fence trapping: *Dermophis parviceps*, *Polychrus gutturosus, Mabuya unimarginata* and *Urotheca decipiens*. In drift-fence arrays, the most captured amphibian was *Dendrobates auratus* (32 captures) followed by *Bufo marinus* (eight captures). The most captured reptile was *Ameiva leptophrys* (54 captures), followed by *Norops cupreus* (14 captures), *Sphenomorphus cherriei* and *Corytophanes cristatus* (11 captures each).

Within Park Site Comparison

Similar amphibian alpha diversity values were observed at sites within PNC (Table 1). Twenty-seven amphibian species were found at HQ, 25 at BFS, and 20 at BC. Eight species were present at all three sites, 17 species shared two sites and 17 species were found at only one. Of the latter, 12 were unique to HQ, three to BFS and two to BC. Amphibian beta diversity was highest between BC and BFS(JSI = 0.552) and lowest between BC and HQ (JSI = 0.237) (Table 3). The family Caeciliidae was only represented at BFS, and no Plethodontidae species were found at the lowland site. Two families (Microhylidae and Dendrobatidae) were found only at the lowland site.

Fifty-five reptile species were observed at HQ, 29 at BFS, and 27 at BC (Table 2). Fourteen reptile species were documented for all three sites, 18 for two sites, and 32 species (primarily snakes) were found at only one site. Of these 32, 27 were unique to HQ, three to BFS and two to BC. The reptile assemblages at BC and BFS were the most similar (JSI = 0.514) (Table 4). Similarity values were lower between HQ and BC (JSI = 0.323) and between HQ and BFS (JSI = 0.333). Six reptile families were restricted to the lowland area (Table 2). At all three sites, the majority of reptile species observed were in the family Colubridae.

Table 3 Comparison between amphibians among three localities within Parque Nacional Carara, Costa Rica. The diagonal shows the total number of species at a locality (N) and the percentage of the overall assemblage found at that site. Figures above the diagonal represent number of species shared between sites (C). Below the diagonal is the Jaccard's Similarity Index.

	Lowland	**Bijagual**	**Bajo Carara**
Lowland	**27 (65.9%)**	14	9
Bijagual	.368	**25 (61.0%)**	16
Bajo Carara	.237	.552	**20 (48.8%)**

Table 4 Comparison between reptiles among three localities within Parque Nacional Carara, Costa Rica. The diagonal shows the total number of species at a locality (N) and the percentage of the overall assemblage found at that site. Figures above the diagonal represent number of species shared between sites (C). Below the diagonal is the Jaccard's Similarity Index.

	Lowland	**Bijagual**	**Bajo Carara**
Lowland	**55 (87.3%)**	21	20
Bijagual	.333	**29 (46.0%)**	19
Bajo Carara	.323	.514	**27 (42.9%)**

Comparison with Dry and Wet Forest

Amphibian alpha diversity at PNC (41 species) was greater than at PNSR (18 species), and slightly less than at Rincón de Osa (46 species) (Table 5). Half the combined species at PNC and Rincon de Osa were shared between the two sites (JSI = 0.554) and just over a quarter were shared (JSI = 0.283) between PNC and PNSR. The amphibian faunas of PNSR and Rincón de Osa however, were very distinct (JSI = 0.123) with only seven species present at both sites.

Alpha diversity among the three sites was more similar for reptiles than amphibians, with PNC found to contain 64 species compared to 54 at SNP and 69 at Rincón de Osa (Table 6). Beta diversity values for reptiles showed the same pattern seen for the amphibian assemblages, with PNC sharing about half the combined species with Rincón de Osa (JSI = 0.446) and one-quarter with PNSR (JSI = 0.255). As for amphibians, PNSR and Rincón were very dissimilar (JSI = 0.108), sharing only 12 species.

Discussion

This is the first study to focus on the herpetofauna of Costa Rica's central pacific coast. This survey of Parque Nacional Carara describes a rich amphibian and reptile fauna that derives its diversity from species found either in wet or dry forests on the Pacific coast of Costa Rica. As such, this chapter presents an example of a transition zone assemblage and allows for the exploration of overall species diversity patterns along this transition zone.

Table 5 Comparison between amphibians among three localities along the Pacific coast of Costa Rica. The diagonal shows the total number of species at a locality (N). Figures above the diagonal represent number of species shared between sites (C). Below the diagonal is the Jaccard's Similarity Index. Data from Parque Nacional Santa Rosa is from Sasa & Solórzano (1995) and data from Rincón de Osa is from McDiarmid & Savage (2005).

	Santa Rosa	**Carara**	**Rincón de Osa**
Santa Rosa	**18**	7	1
Carara	.283	**41**	25
Rincón de Osa	.123	.554	**46**

Table 6 Comparison between reptiles among three localities along the Pacific coast of Costa Rica. The diagonal shows the total number of species at a locality (N). Figures above the diagonal represent number of species shared between sites (C). Below the diagonal is the Jaccard's Similarity Index. Data from Parque Nacional Santa Rosa is from Sasa & Solórzano (1995) and data from Rincón de Osa is from McDiarmid & Savage (2005).

	Santa Rosa	**Carara**	**Rincón de Osa**
Santa Rosa	**54**	14	2
Carara	.255	**64**	31
Rincón de Osa	.108	.446	**69**

Overall, PNC diversity was characterized by high alpha diversity in the lowland site, with fewer, but different, species found in the two highland sites. Thus, alpha diversity at HQ and within-park beta diversity underlie the park's overall diversity. Differences in diversity among sites within PNC may be due to changes in elevation and associated changes in climate and vegetation. Additionally, the proximity of the BFS and BC to open farmlands and pasture could cause edge effects that affect presence of some species at those sites. Much of the difference in within-park assemblages was due to lowland species restricted to the HQ site (e.g. species in the families Microhylidae, Dendrobatidae and Iguanidae), Gymnophiona and Caudata being restricted to higher elevations, and the HQ site having greater alpha diversity in higher-order taxon groups shared with other sites. For instance, out of the 11 hylid species found in PNC, five were found at all three sites, but HQ had an additional five species.

Sampling bias may also account for some differences in species diversity between sites. More person-days were spent sampling lowland areas (HQ) than elsewhere, and 84.5% of the drift fence sampling occurred there. The remaining 15.5% of drift fence sampling was done only at BFS. Sampling at BC, the most remote site, consisted of 77 person-days in January 2001. Furthermore, sampling at Bajo Carara was during the dry season, possibly limiting the number of amphibians encountered, although several streams and a lagoon were surveyed. Future sampling efforts at PNC would benefit prolonged sampling at Bajo Carara during the rainy season. Differences in sampling effort probably affected the capture of snake species, which are rare, secretive

and the hardest to sample. This helps explain the higher number of snakes reported for the lowland (HQ) area.

Comparison of PNC to the Dry and Wet Forests

Carara's amphibian and reptile assemblage was intermediate, in both species numbers and composition, between the dry forest to the north and the wet forest to the south. Although PNC contained herpetofaunal elements from both regions, the combination of species there was clearly distinct. Differences between PNC and PNSR amphibian alpha and beta diversity values were due to a lack of salamanders and Centrolenidae at PNSR, as well as fewer Hylid and *Eleutherodactylus* species there. Differences in diversity components between PNC and Rincón were due primarily to fewer Dendrobatidae species at PNC and the inclusion of dry forest species at PNC that were absent from Rincón de Osa.

A large number of dry-forest snake species at PNSR drove alpha diversity of reptiles at that site. The pattern of beta diversity we observed resulted from sets of species that were shared between PNC and PNSR, and PNC and Rincón. Beta diversity was high between PNSR and Rincón de Osa, and each of those sites shared very few species of either amphibians or reptiles. One interesting exception was the frog, *Physalaemus pustulosus*, found in both northwest and southwest Costa Rica yet absent from the central pacific coast. Parque Nacional Carara shared roughly twice as many species of amphibians and reptiles with Rincón, making it more similar to the pacific lowland rain forest than the tropical dry forest.

Faunal Zone Analysis

It seems the transitional assemblage of PNC serves as a boundary for species from both faunal units. Six amphibian and five reptile species representative of the southwestern wet forest assemblage, for example, reach the northernmost known extent of their range at PNC. Additionally, one amphibian and three reptile species representative of the northwestern tropical dry forest assemblage, reach the southernmost known extent of their range at PNC (Savage, 2002).

A review of Savage's (2002) herpetofaunal areas corroborates the results from the analysis of diversity components presented in this chapter and further demonstrates the blending of herpetofaunas that created the transition assemblage at PNC. Geographically, PNC lies near the border of Savage's (2002) northwest and southwest faunal areas. Savage characterized the northwest faunal area by an equal proportion of Old Northern Element (ON) and Middle American Element (MA) genera (36:34%) and the southwest faunal area by similar proportions of MA to South American Element (SA) genera (37:33%). Of the 63 native genera found at PNC, 34.4% correspond to ON, 40.6% to the ME and 23.4% to SA (Table 7). Parque Nacional Carara's proportions of ON to MA (34:41%) and ON to SA (41:23%) do not correspond to either the northwest or southwest faunal areas, because PNC contains a high proportion of Middle American genera that correspond to the northwestern fauna area, and relatively few South American genera corresponding to the southwest faunal area.

Although the herpetofauna of PNC is clearly transitional, it represents one locality along the central pacific coast, and therefore it is difficult to comment on species

Table 7 Origin of the genera of herpetofauna of Parque Nacional Carara, Costa Rica. Principal Historical Assemblages of Central American Herpetofauna follow Savage (2002).

Genera	Old Northern Elements	Tropical Middle America	Tropical South America
AMPHIBIA (17)			
Gymnophiona (1)			
Dermophis		+	
Caudata (2)			
Bolitoglossa	+		
Oedipina	+		
Anura (14)			
Agalychnis		+	
Bufo		+	
Centrolene			+
Cochranella			+
Dendrobates			+
Eleutherodactylus		+	
Hyalinobatrachium			+
Hyla		+	
Hypopachus		+	
Leptodactylus			+
Phrynohyas			+
Rana	+		
Scinax			+
Smilisca		+	
REPTILIA (47)			
Crocodylia (1)			
Crocodylus		+	
Testudinata (2)			
Kinosternon	+		
Rhinoclemmys	+		

Table 7 continued

Genera	Old Northern Elements	Tropical Middle America	Tropical South America
Sauria (18)			
Ameiva			+
Basiliscus		+	
Cnemidophorus	+		
Coleonyx	+		
Corytophanes		+	
Ctenosaura		+	
Gonatodes		+	
Hemidactylus			
Iguana		+	
Lepidoblepharis			+
Lepidophyma	+		
Leposoma			+
Mabuya	+		
Norops		+	
Polychrus			+
Sphaerodactylus		+	
Sphenomorphus	+		
Thecadactylus			+
Sauria (26)			
Boa		+	
Bothriechis	+		
Bothrops	+		
Coniophanes		+	
Dendrophidion	+		
Drymobius	+		
Enulius		+	
Geophis		+	
Hydromorphus		+	
Imantodes		+	
Lampropeltis	+		
Leptodeira		+	
Leptophis	+		
Masticophis	+		
Mastigodryas	+		

Table 7 continued

Genera	Old Northern Elements	Tropical Middle America	Tropical South America
Micrurus			+
Ninia		+	
Oxybelis	+		
Oxyrhopus			+
Pseustes	+		
Rhadinaea		+	
Sibon		+	
Spilotes	+		
Tantilla	+		
Tripanurgos			+
Urotheca		+	

diversity patterns and species turnover rates along the entire transition zone. Further work will focus on filling in the knowledge gaps along the entire central pacific coast of Costa Rica in order to further investigate the rate and pattern of turnover in herpetofaunal species along the entire pacific coast.

Implications for Conservation

Parque Nacional Carara supports a rich herpetofauna of over 100 species composed of both dry and wet forest elements thus exhibiting a unique faunal assemblage. As the largest track of protected forest in an area mostly converted to farmland or pasture, PNC is possibly the last refuge for many of these species in the region. Fortunately, the future of PNC as a protected area seems secure. Created as a biological reserve in 1978, and converted to a national park in 1999 to facilitate tourism, PNC is currently one of the country's most visited parks. Its rich flora and fauna and proximity to San José and the cruise ship dock of Puntarenas draw large numbers of tourists. Adding to its appeal, Carara is home to one of two remaining significant Scarlet Macaw (*Ara macao*) populations in the country (Vaughan *et al.,* 1991) and it boasts the country's most accessible site for viewing American Crocodiles (*Crocodylus acutus*). Appreciation for the natural resources of PNC will be enhanced by understanding the makeup of biodiversity found there. Indeed the results of this study will be incorporated into outreach materials for the park. Additionally, I hope this study will serve as a springboard for future research of Costa Rica's central pacific coast allowing PNC to serve as a living laboratory for the discovery and conservation of the region.

CHAPTER IV

HERPETOFAUNAL INVENTORY OF FOUR SITES IN THE EASTERN PORTION OF THE ÁREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

Synopsis

The Área de Conservación Guanacaste, located in far northwest Costa Rica, is famous for its protection of the largest remaining tract of dry forest habitat in Central America. However, the area also contains lesser-known, more mesic habitats in its eastern portion. Between June and August 2001 amphibian and reptile inventories were conducted in four sites located in the eastern portion of the Área de Conservación Guanacaste (ACG). A total of 35 amphibians and 54 reptile species were documented. Of the four sites studied, Estación Caribe in the newly purchased Rincon Rainforest was the most species rich (52 species). The Rincon Rainforest is important in providing habitat for amphibians and reptiles. Volcán Cacao is particularly rich in snake species; however, more sampling is needed to provide a full assessment of its total herpetological diversity.

Introduction

Growing concern over the rapid loss of biodiversity due to habitat loss around the world has led to an increased awareness of the necessity for biological inventories (Raven & Wilson, 1992). Inventories provide a basis on which to plan conservation and

land use strategies, and they contribute directly to the development of new crops, pharmaceuticals, and the advancement of allied disciplines of science (Raven & Wilson, 1992). They also help to justify conservation projects by highlighting the diversity of a protected or potentially protected area. Costa Rica's Área de Conservación Guanacaste (ACG), a world heritage site, is one of the country's most celebrated and studied areas (Janzen, 1986). Although some information is available for biodiversity of the area, there is a lack of knowledge about the local herpetofauna. Herpetological work in the ACG has focused on the dry forest of Parque Nacional Santa Rosa (Sasa & Solórzano, 1995). The eastern more mesic sectors have yet to receive the same attention. The purpose of this study is to provide baseline information on the amphibian and reptile species present in these sectors of the ACG. Two recently created areas were of special interest: the Rincon Rainforest (RR), and the Rincon-Cacao corridor (RCC). The RR acquisition is an ongoing project begun in 1998 to purchase available land contiguous with existing park land to extend the ACG. The area was once used for timber extraction, bean fields, small pastures and homesteads, but is now vacant and being purchased to become part of the ACG and be incorporated into the National Parks System of Costa Rica (Janzen & Hallwachs, 2006). Over 98.52% of the available Rincon Rainforest lands had been purchased by 31 March 2006 (Janzen & Hallwachs, 2006). The RCC consists of land purchased between 1992-1998 linking Volcán Rincón de la Vieja and Volcán Cacao. These parcels serve as a biological corridor between the two volcanoes and between the rainforests in the eastern ACG and the dry forest to the west. Furthermore, they unified the ACG into one contiguous protected area. This paper

will present species lists from four sites within the ACG and provide a brief comparison of each site. Furthermore, I will comment on the conservation value of the newly purchased Rincon Rainforest in terms of amphibians and reptiles.

Methods

Study Sites

Four sites throughout the eastern ACG were surveyed (Fig. 2): Estación Caribe (EC), Estación San Gerardo (SG), Gavilán and Estación Biológica Cacao (EBC). Estación Caribe is located in the RR proper and SG falls within the RCC. Gavilán lies just to the north of the RR and west of Estación Caribe. Estación Biológica Cacao, located on the inactive Volcán Cacao, is a highland site containing cloud forest and as such is distinct from the other three sites.

Estación Caribe

Situated within the RR, Estación Caribe is a station currently utilized by parabiologists. In its entirety, the RR is a 5,600-hectare piece of land consisting of premontane rainforest at 900 m elevation down to very humid rainforest at 200 m elevation (Holdridge, 1967); it receives 4 - 5 m of rainfall annually (Janzen & Hallwachs, 2006). The elevation of EC and the surrounding area range from 365 to 390 m, and the area is classified as tropical moist forest transition to very moist forest (Holdridge, 1967). The most important feature at this site is the Rió Francia, which runs near the station and is surrounded by primary forest. The lands around EC also include regenerating farmland, wetlands and secondary rainforest.

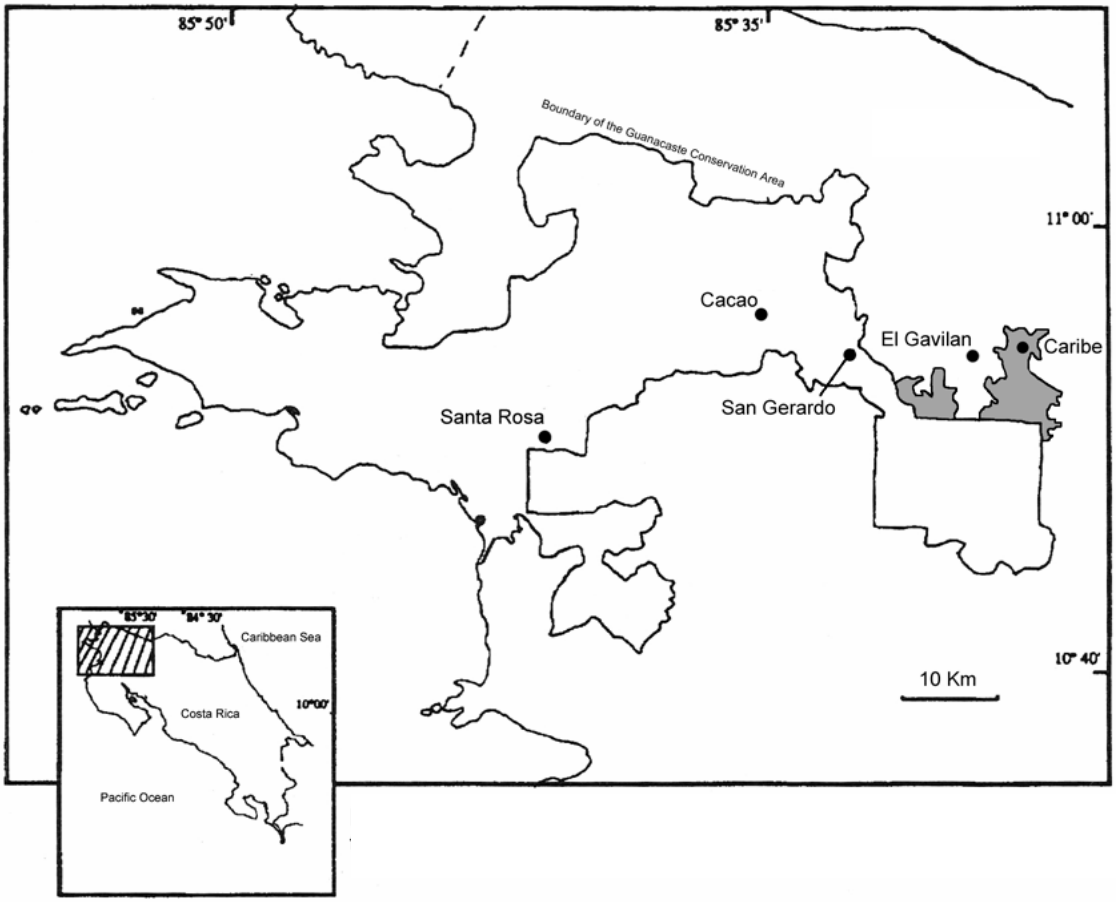

Figure 2 Map of the Área de Conservación Guanacaste, Costa Rica. The Rincon Rainforest is shaded in gray and four sample sites are shown.

Estación San Gerardo

Located within the RCC, Estación San Gerardo, classified as tropical moist forest transition to very moist forest (Holdridge, 1967), consists of a small patch of secondary forest along a mountainside with an elevation of approximately 600 to 700 m. There are considerable open areas around the station as well as ditches and pools along the road that runs in front of the station. Several small creeks run through the site, one of which was dammed to create a pond. Included as part of this site was the town of Dos Rios, located 2 km west of the station as well as the area in between.

Gavilán

The area designated as the Gavilán site spans from the town of Gavilán east to the Rio Negro. This area is classified as tropical moist forest transition to very moist forest (Holdridge, 1967) and contains several rivers and streams. At least two of the rivers flow north from the active Volcán Rincón de la Vieja and are "sterile" due to high levels of noxious runoff from the volcano. Gavilán is characterized by many farms mixed with forest. Most of the forest is riparian or secondary growth. There were also open grassy areas with standing water as well as several small ponds.

Estación Biológica Cacao

Volcán Cacao is an inactive volcano located at the north end of the RCC, northwest of Dos Ríos. Estación Biológica Cacao lies at 1100 m elevation and serves as trailhead to a series of trails. At EBC sampling took place from the Rió Góngora at approximately 800 m elevation up to the summit of the volcano at an elevation of 1659

m. Habitat in the area consists of intermediate elevation primary rainforest and cloud forest (Holdridge, 1967) and contained several streams.

Survey Methods and Data Analysis

Data were collected from 22 June to 9 August 2001, corresponding with the rainy season. The primary collecting method was diurnal and nocturnal visual encounter surveys (VES) (Crump & Scott, 1994). Groups of one to ten individuals searched an area and recorded each individual amphibian and reptile observed. Time spent searching was also recorded. Because the VES had varying numbers of participants and varying search duration, all VES data were transformed to encounters/person hour. Species were also collected opportunistically and by road cruising. Uneven sampling among sites makes the comparison of species richness difficult. To allow for equal comparisons rarefaction curves were calculated using Ecosym version 7.72 (Gotelli & Entsminger, 2001). These curves provide comparable expected species numbers, derived from 1000 Monte Carlo simulations for each site. The simulations are based on the fewest number of observations among sites so that species richness values are based on the same number of observations at each site. Voucher specimens for each species were deposited at the Museum of Zoology of the University of Costa Rica (UCR). Tissue samples were deposited in the frozen tissue collection at Texas State University, San Marcos, Texas, USA. Parasites were removed from specimens collected from 22 – 28 June and preserved by a team of parasitologists. Parasite specimens were deposited at the University of Toronto.

Results

A total of 723 individuals comprising 89 species were documented for the eastern ACG, including one caecilian, one salamander, 33 frog, two turtle, 19 lizard, and 33 snake species (Tables 8 and 9). Three species: *Boa constrictor, Spilotes pullatus* and *Drymarchon corais* were not captured but were identified in the field and are included in the list. Additionally, *Dactyloa insignis* was identified from a photograph provided by Dr. Dan Janzen (pers comm.) and two other local species, *Chelydra serpentina* and *Porthidium ophryomegas*, were identified at a small zoo near Gavilán.

A total of 455 person-hours were spent conducting VES, during which 395 amphibians and 328 reptiles were encountered. The overall encounter rate was 1.58 encounters/person-hour. However, search effort and encounter rates varied among sites. Search effort in terms of person-hours was highest for Estación Caribe and the lowest at Estación Biológica Cacao. Variance in search effort also affected the perceived completeness of the survey for each site, as indicated by the steepness of species-accumulation curves (Fig. 3). Overall, the most encountered amphibians included *Bufo marinus* (39 observations), *Rana warschewitschii* (36 observations) and *Smilisca baudinii* (36 observations), but the most encountered species was by far the lizard *Norops oxylophus* with 150 observations. This species was also the most frequently encountered lizard species at each of the four sites. Other common lizards included *N. humilis* (41 observations), *N. limifrons* (21 observations) and *N. capito* (17 observations). Overall, the six anole species (232 observations) accounted for 32.1% of

Table 8 Amphibian abundance, habitat, and time of activity for four sites in eastern Área de Conservación Guanacaste, Costa Rica. Abundance categories follow Rand & Myers (1990). Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen. Habitat: Fos = fossorial, under leaf litter or under ground; Ter = terrestrial, ground or litter; Arb = bush, forest understory. Time of activity: D = diurnal, N = nocturnal.

	Abundance				**Habitat**	**Time of Activity**
	Gavilán	San Gerardo	Caribe	Cacao		
Caeciliidae (1)						
Gymnopis multiplicata			R		Fos	N?
Plethodontidae (1)						
Bolitoglossa striatula			I		Ter	N
Leptodactylidae (9)						
Eleutherodactylus bransfordii	R				Ter	D
Eleutherodactylus cerasinus		R			Ter	D
Eleutherodactylus cuaquero				R	Ter	D
Eleutherodactylus diastema	C	C	C	C	Arb	N
Eleutherodactylus fitzingeri	C	C	C		Ter,Arb	D
Eleutherodactylus ridens		R		R	Ter	D
Eleutherodactylus stejnegerianus				R	Ter	D
Leptodactylus labialis	R	U	U		Ter	DN
Leptodactylus melanonotus	U	U	U	I	Ter	DN
Bufonidae (4)						
Bufo haematiticus	U		U		Ter	N
Bufo marinus	C	C	C	C	Ter	N
Bufo melanochlorus	R				Ter	N
Bufo valliceps	U		I		Ter	N
Hylidae (12)						
Agalychnis callidryas	C	I	U	R	Arb	N
Duellmanohyla rufioculis	R			R	Arb	N
Hyla ebraccata	U	I			Arb	N
Hyla loquax	I	R	I		Arb	N
Hyla microcephala	U	I	I	R	Arb	N
Hyla rufitela			U		Arb	N
Phrynohyas venulosa				R	Arb	N
Scinax boulengeri	I		R		Arb	N
Scinax elaeochroa	C	U	U		Arb	N
Scinax staufferi			R	R	Arb	N
Smilisca baudinii	C	U	I		Arb,Ter	N
Smilisca puma	U		U		Arb	N
Dendrobatidae (1)						
Dendrobates pumilio	I		I		Ter	D

Table 8 continued

	Abundance				Habitat	Time of Activity
	Gavilán	San Gerardo	Caribe	Cacao		
Centrolenidae (3)						
Cochranella granulosa			R	*	Arb	N
Cochranella spinosa			I		Arb	N
Hyalinobatrachium fleischmanni			U	**	Arb	N
Ranidae (4)						
Rana forreri	R	R		R	Ter	N
Rana taylori	C	U	U		Ter	N
Rana vaillanti	I	C	I		Ter	N
Rana warschewitschii	C	I	U	R	Ter	N

Table 9 Reptile abundance, habitat, and time of activity for four sites in eastern Area de Conservación Guanacaste, Costa Rica. Abundance categories follow Rand & Myers (1990). Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen. Habitat: Fos = fossorial; Ter = terrestrial, ground or litter; Arb = bush, forest understory; Can = canopy; Aq = aquatic; AqMar = aquatic margin; Bld = man made structures. Time of activity: D = diurnal; N = nocturnal.

	Abundance				**Habitat**	**Time of Activity**
	Gavilán	San Gerardo	Caribe	Cacao		
Chelydridae (1)						
Chelydra serpentina	R				Aq	DN
Kinosternidae (1)						
Kinosternon leucostomum	I				Aq	DN
Gekkonidae (4)						
Gonatodes albogularis			R		Arb,Bld	D
Sphaerodactylus homolepis		R			Ter,Bld	D
Sphaerodactylus millepunctatus		I	I		Ter,Bld	D
Thecadactylus rapicauda	R		I		Arb	N
Corytophanidae (2)						
Basiliscus plumifrons	I		I		AqMar	D
Corytophanes cristatus	R	C	I		Ter	N
Iguanidae (1)						
Iguana iguana	R		R		Can	D
Phrynosomatidae (1)						
Sceloporus variabilis				R	Ter	D
Polychrotidae (7)						
Dactyloa insignis		R			Can?	?
Norops biporcatus	I		I	*	Arb	D
Norops capito	U	U	R	R	Ter	D
Norops humilis	U	U	I	R	Ter	D
Norops lemurinus	R		R		Can?,Bld	D
Norops limifrons	U	I	I		Arb	D
Norops oxylophus	U	C	C	R	AqMar	D
Teiidae (2)						
Ameiva festiva	I		U		Ter	D
Ameiva undulata				**	Ter	D
Scincidae (2)						
Mabuya unimarginata				R	Ter	D
Sphenomorphus cherriei			R	R	Ter	D
Boidae (2)						
Boa constrictor	R		*		Arb,Ter	DN
Corallus annulatus	R		R		Can	N

Table 9 continued

	Abundance				Habitat	Time of Activity
	Gavilán	San Gerardo	Caribe	Cacao		
Colubridae (23)						
Chironius grandisquamis			R		Arb	N
Dendrophidion vinitor				R	Ter	D
Dipsas bicolor		R		R	Arb	N
Drymarchon corais			**		Ter	D
Drymobius melanotropis				R	Ter	N
Erythrolamprus mimus		R		*	Ter	N
Geophis hoffmanni				R	Ter	N
Geophis zeledoni				R	Ter	N
Hydromorphus concolor			R		Aq	N
Imantodes cenchoa		I	I	R	Arb	N
Leptodeira septentrionalis			R		Arb,AqMar	N
Leptophis depressirostris	R				Arb	D
Leptophis nebulosus			R		Arb	D
Mastigodryas melanolomus			R		Ter	D
Ninia maculata		I		I	Ter	N
Oxyrhopus petolarius	R				Ter	N
Sibon dimidiatus				R	Arb	N
Sibon nebulatus	I		I		Arb,Ter	N
Spilotes pullatus	*				T,Arb	D
Urotheca euryzona	R	R			Ter	N
Urotheca guentheri				R	Ter	N?
Urotheca pachyura				R	Ter	N
Xenodon rabdocephalus			R		Ter	D
Elapidae (2)						
Micrurus alleni	R				Ter	ND
Micrurus nigrocinctus	R				Ter	ND
Viperidae (6)						
Atropoides nummifer		I		R	Ter	N
Bothriechis lateralis				R	Arb,Ter	N
Bothriechis schlegelii		C	R	R	Arb,Ter	N
Bothrops asper	R		R		Ter	N
Crotalus durissus				**	Ter	N
Porthidium nasutum	***				Ter	N

* Seen and identified, but not captured.
** Previously caught and preserved by workers on the mountain.
*** Caught in the area and being held at a local zoo.

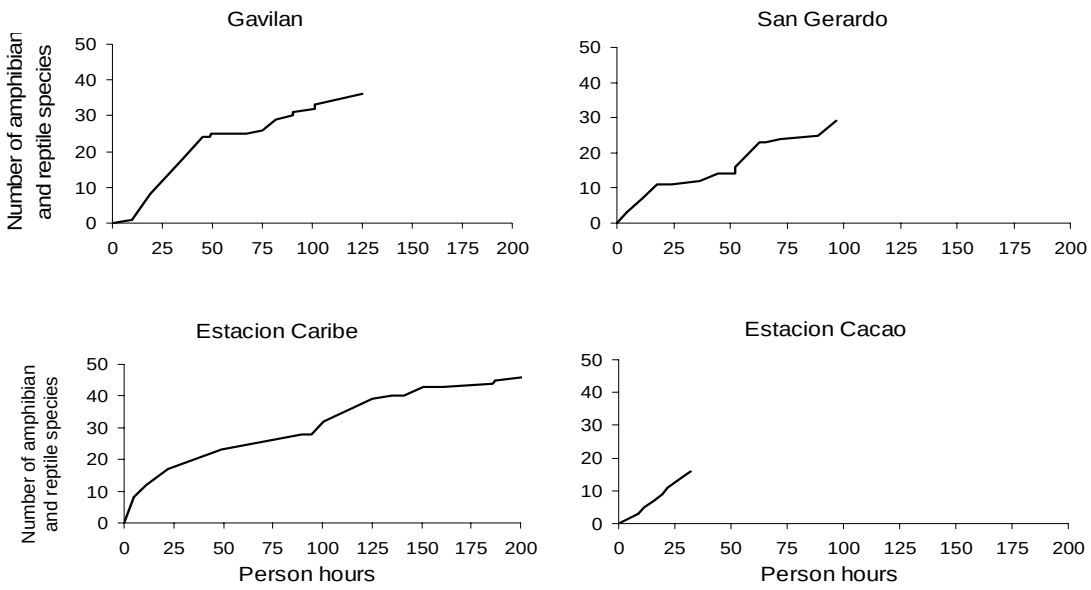

Figure 3 Rate of amphibian and reptile species accumulation for four sites in the eastern Área de Conservación Guanacaste, Costa Rica The four sites are Gavilán, San Gerardo, Estación Caribe and Estación Cacao.

all observations. The most frequently encountered snake was *Bothriechis schlegelii* (21 observations) which was common at SG.

Estación Caribe

Three hundred one observations were recorded over the 200.9 person-hours spent conducting VES at EC for a rate of 1.5 encounters/person hour. Of these observations, 193 were of amphibians (25 species) and 108 were of reptiles (27 species). The 52 species found at EC made it the most species rich site surveyed. The site's diversity was concentrated in two areas, the Rió Francia and its gallery forest, and in numerous lagoons and flooded low areas. Lizard and snake diversity was highest at the former while amphibian diversity peaked in and around the latter. All groups found in the eastern ACG were found at EC except turtles. The only caecilian found during the inventory was found near the Rió Francia after a heavy rain. All frog species collected at EC were observed calling; egg masses were found for *Cochranella granulosa, C. spinosa*, *Hyalinobatrachium fleischmanni,* and *Agalychnis callidryas*.

San Gerardo

One hundred and seventy observations were recorded for SG over 96.9 person/hours. An encounter rate of 1.75 encounters/person hours produced 17 anuran, eight lizard and seven snake species. San Gerardo was defined by its high abundance of *Bothriechis schlegelii*. Seventeen individuals were observed in eight days of sampling making this the most frequently observed snake in any area. The most frequently observed lizards at SG were *Norops oxylophus* (55 observations) and *Norops humilis* (15

observations). All *N. oxylophus* were observed along stream margins and the *N. humilis* on the forest floor. The population of *Corytophanes cristatus* at SG was noteworthy as well. While relatively few individuals (eight) were observed, they accounted for 57% of all observations of this species in the region. Anuran species in this area were found in both the forest and in open grassy pasture areas with standing water. The most abundant frog species at SG was *Smilisca baudinii* (13 observations).

Gavilán

Forty-seven species were documented for Gavilán, included 23 frog, two turtle, 11 lizard and 11 snake species. One hundred eighty eight observations were recorded over 125.2 person hours for a rate of 1.50 observations/person hour. Gavilán's high anuran diversity was centered in marshy areas with high grass and in two small ponds. The most frequently encountered frog species were *Rana warschewitschii* and *Hyla ebraccata* (16 observations each) followed by *Rana taylori* (11 observations) and *Smilisca baudinii* and *Bufo marinus* (10 observations each). Gavilán was the only site where the turtles, *Chelydra serpentina* and *Kinosternon leucostomum* were found. The site also marked the westernmost sighting of a *Dendrobates pumilio*, and the easternmost sighting of a *Rana forreri*. This site contained the 'sterile', Rió Azul that indeed appeared void of vertebrate life. An adult *Spilotes pullatus* was seen along the bank of Rió Azul, but was not captured. There was a noted lack of *Eleutherodactylus* species in this area.

Estación Biológica Cacao

Estación Biológica Cacao, in contrast to Gavilán, had high *Eleutherodactylus* diversity (four species) although total amphibian diversity was low (15 species). The *Eleutherodactylus* diversity includes a new locality for *Eleutherodactylus cuaquero*, previously known only from Monteverde. Snake diversity at EBC was the highest of all sites with 15 species observed. This diversity is exceptional given the small amount of time spent at the site In 32.0 person/hours of VES 64 observations of 23 species were made giving a rate of 2.00 species/person hour, the highest collecting rate of any site. Furthermore, many snake species observed at EBC were observed nowhere else. These include: *Dendrophidion vinitor, Drymobius melanotropis, Geophis hoffmanni, G. zeledoni, Sibon dimidiatus, Urotheca guentheri, U. pachyura, Bothriechis lateralis* and *Crotalus durissus.* The last species was identified from a preserved specimen at EBC. Lizard diversity at EBC was not high (eight species) but two species were only observed at this site: *Sceloporus variabilis* and *Mabuya unimarginata*.

Discussion

Our surveys of four sites in eastern ACG provide evidence that the region is high in herpetological species richness. Overall, the region contained more species (89 species) than Parque Nacional Santa Rosa (78 species) (Sasa & Solórzano, 1995). Species richness varied by site, but so did the completeness of surveys (Fig. 3). Hence, it is difficult to interpret differences in species richness among sites. Estación Caribe had the greatest species richness, for example, but we also spent the most person-hours searching there. The EC species accumulation curve has begun to flatten, indicating that

much more collecting effort would be required to find additional species. Conversely, undetected species should be found with relatively little additional effort at San Gerardo, and especially at EBC.

The rarefaction curves corroborate the results of the species accumulation curves. They show that EC is more diverse that the other sites based on the number of species expected in samples of equal size. Thus, EC's higher species richness truly exists and is not a result of greater sampling (Fig. 4). Furthermore, the slopes of the rarefaction curves show that more species should be expected at all sites, and agree with the species accumulation curves in that EBC should be the site with the highest remaining number of species to be found with additional effort.

Although not complete, the list allows generalizations to be made about habitat affinities of species, and comparisons to be made among the sites. Estación Caribe, the closest to lowland rainforest, contained the highest diversity despite little forest cover in the area. The high species richness in the area can be attributed to species associated with the Rió Francia corridor, where we found the majority of species documented for the EC. The San Gerardo and Gavilán sites had fewer species. The lower numbers there can be attributed to small forest patches, increased human habitation and agriculture, as well as the 'sterile' rivers that receive effluents from the Rincon de la Vieja volcano. The inventory of Estación Biológica Cacao produced interesting results that warrant further investigation. The findings showed lower overall amphibian and lizard diversity at EBC than the other sites, but diversity of *Eleutherodactylus* frogs was high and snake diversity was greater than all other sites. In addition, the EBC encounters/person-hour

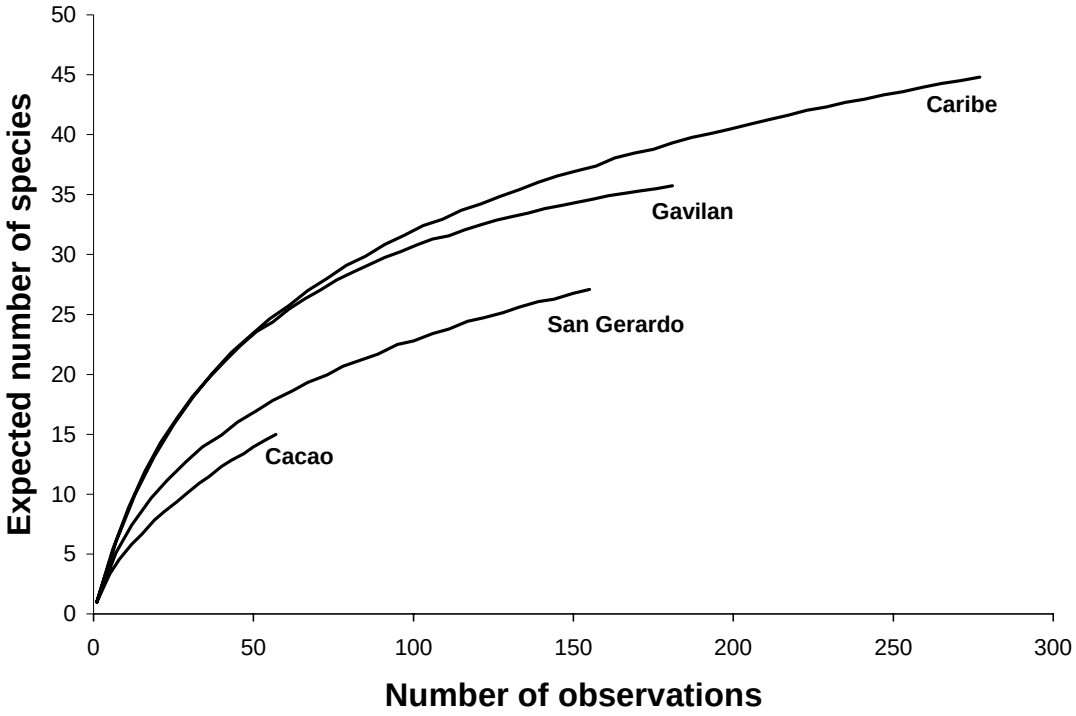

Figure 4 Species rarefaction curves of the expected number of species detected for four sites in the eastern Área de Conservación Guanacaste, Costa Rica based on number of observations.

rate was higher (2.0 encounters/person-hour) than all other sites and the species area curve indicates many additional species could be documented for this site. The EBC site may in fact turn out to be one of the area's most diverse sites in terms of amphibians and reptiles. According to Dr. Daniel Janzen (pers comm.), herpetological biodiversity has declined drastically over the last thirty years. Without a baseline species list for comparison, it is impossible to determine whether a decline in herp species richness has occurred in this region. That not withstanding, the high encounter rate, unique fauna of the site within the area and the existence of species which are known from areas that have seen declines recently, provide good reasons for continued collecting efforts at EBC.

One thing is for certain, the newly established areas of the Rincon-Cacao Corridor and the Rincon Rainforest, along with Volcán Cacao, provide important protected habitat, which help preserve the rich herpetological diversity in the Northern portion of Costa Rica.

CHAPTER V

INVENTORY OF THE AMPHIBIANS AND REPTILES OF RESERVA NATURAL ABSOLUTA CABO BLANCO, COSTA RICA

Synopsis

A survey of the amphibians and reptiles of Reserva Natural Absoluta Cabo Blanco, Puntarenas, Costa Rica was conducted from May to August 2003. Thirteen amphibian and 19 reptile species were found within the park's boundaries. Twenty-two of these species were not previously recorded from the lower Nicoya Peninsula and for seven this locality represents the southernmost extension of their range. One additional amphibian and three reptile species are known from the area based on literature review and examination of museum collections. However, interviews with locals indicate up to nine other reptile species could be present in the reserve. I observed all but one amphibian species at Laguna Balsitas and at least eight species utilize the lagoon for reproduction. The lagoon is also notable for its population of *Kinosternon scorpioides.* . This study will provide a baseline for further research in the reserve.

Introduction

The importance of herpetological inventories as a basis for planning conservation and land use strategies, and as a springboard for future research, has been noted by several authors (Raven & Wilson, 1992; DaSilva & Sites, 1995; Sasa & Solórzano, 1995). In Costa Rica, there is a long history of herpetological inventories, most notably

the work by Savage and his students spanning almost 40 years (Scott *et al.*, 1983; Donnelly, 1994; Guyer, 1994; McDiarmid & Savage, 2005), and that of Sasa & Solórzano (1995). Despite this long and productive effort, the herpetofauna in many areas around the country remains undocumented. Such is the case with the Reserva Natural Absoluta Cabo Blanco (RNACB). Established in 1963, RNACB has the distinction of being Costa Rica's first protected area. As such, it holds an important place in Costa Rican conservation both as an Absolute Reserve and as a symbol of the country's commitment to conservation. To date however, no formal list of its amphibians and reptiles exists.

In this chapter, I present the results of a three-month inventory of RNACB and provide a preliminary species list of its amphibians and reptiles. I also compare the list of species found in the reserve to known records of herp species in the Cabo Blanco area. Comments follow regarding the abundance, distribution within the reserve, and natural history of these species. This list is by no means final and is presented as a baseline to build upon and to stimulate future study in the area.

Methods

Study Site

Reserva Natural Absoluta Cabo Blanco, lying at the southern tip of Costa Rica's Nicoya Peninsula (9°34' N, 85°5'W) (Fig. 5), comprises 1270 terrestrial hectares and 1700 ha of marine area. Known for its marine bird populations, the reserve ranges in elevation from sea level to 359 m (Boza, 1984), and is part of the Tempisque Conservation Area. At its creation, eighty-five percent of its lands were being used for

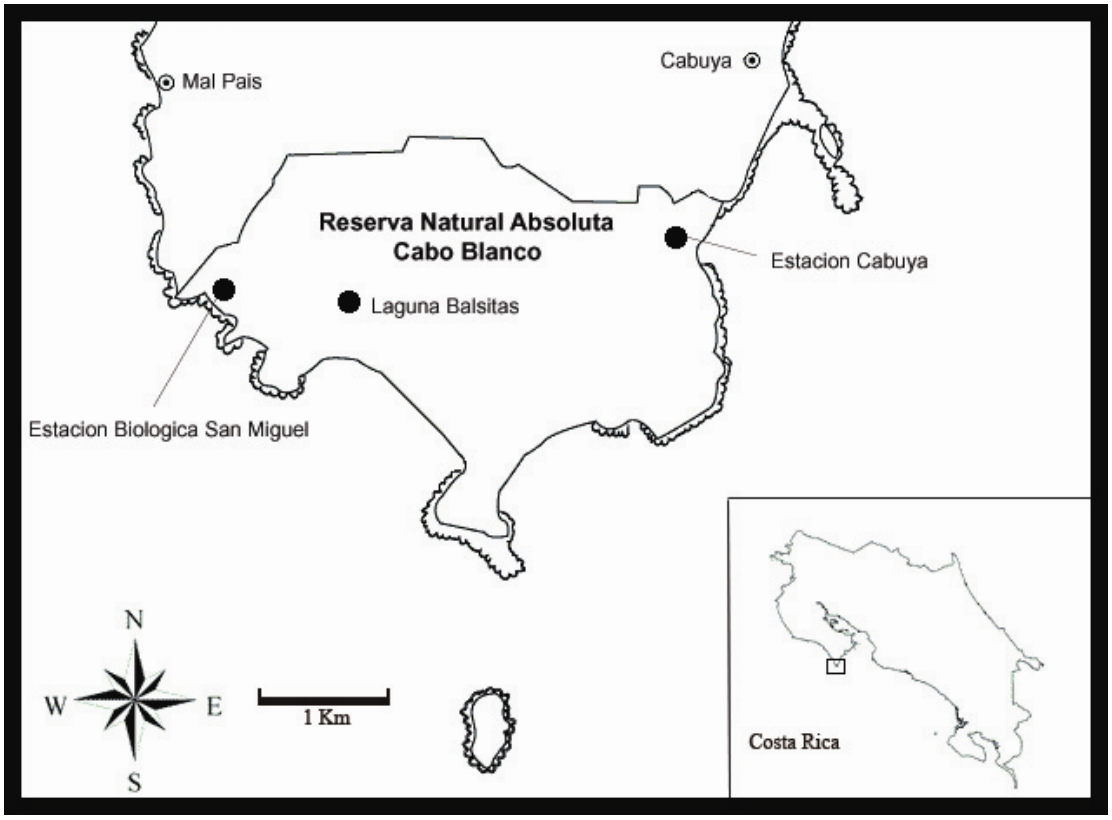

Figure 5 Map of Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica. The three sampling localities within the reserve are named and denoted by black circles.

agriculture or grazing and were therefore deforested. However, over the last 40 years, much of the natural vegetation in the RNACB has regenerated, and today the reserve consists of a mixture of primary and secondary forest. Holdridge's (1967) life zone system classifies RNACB as tropical moist forest and the reserve's mean annual temperature is 27.25° C (SINAC, 2002). Mean yearly rainfall is 2895.4 mm, most of which falls between May and November (Instituto Meteorológico Nacional: Promedios Mensuales de Datos Climáticos: Estación Cabuya, 1985). The reserve has several streams, the two most important being Quebrada San Miguel and Quebrada Cabo Blanco.

This study focused on three areas within the reserve (Fig. 5): Estación Cabuya (ECB), Estación Biológica San Miguel (EBSM) and Laguna Balsitas (LB). Estación Cabuya (9°35'21"N, 85°5'34.0W) lies on the eastern side of the reserve and serves as the reserve's administrative center as well as the trailhead for the public trails. The lands around the station include open areas, human habitations, beaches and an open, grassy arboretum. Sendero Sueco leaves ECB and heads south through the forest for 4 km towards the tip of the peninsula, crossing Quebrada Cabo Blanco twice. Also of interest at ECB are the roads leading to the station from the North that contain ephemeral pools housed in tire ruts and depressions. Estación Biológica San Miguel (9°34'47.5"N, 85°8'12.6"W), located on the west side of the reserve facing the Pacific Ocean, serves as the main investigative center and consists of a main house, dorm, laboratory and associated buildings. The surrounding area consists of regenerating forest with open sunny areas. EBSM is located next to Quebrada San Miguel and serves as the trailhead

to Sendero Maven and Sendero El Barco. Leaving EBSN to the North is a small road to Mal País, which also contained ephemeral pools that provided suitable reproductive habitat for the area's amphibians. Laguna Balsitas (9°34'50.1"N, 85°7'28.6"W) is an ephemeral lagoon located in the reserve's interior to the west of EBSM along Sendero Central. The lagoon is approximately 40 m X 50 m, filled with high grass and surrounded by forest. A small stream feeds the lagoon, which increased in size continuously throughout this study. On the first visit to the lagoon on 6 June, it was no more than a small puddle surrounded by a larger area of soft mud. By 20 June, it had expanded to a 15 m X 15 m pool. By mid August, the lagoon had grown to an approximate 35 m X 50 m with depths exceeding 2.75 m in some areas.

Capture Methods

This study took place between 30 May and 17 August 2003, corresponding to the beginning of the rainy season in the area. I used drift fence arrays and visual encounter surveys to sample amphibians and reptiles. Three drift fence arrays, two near the EBSM and one at LB, were constructed following Corn (1994). Array arms were 15 m in length and constructed using polystyrene as described by Malone & Laurencio (2004). I constructed all of the arrays in a "Y" formation. For the two EBSM arrays, 20 L buckets were sunk at the end of each arm and in the middle of the array, and a 22.9 cm x 44.5 cm Gee Minnow Trap was placed on either side of each arm at the midway point, for a total of ten traps per array. At Laguna Balsitas, the array was set up in a similar fashion, but with two double and one triple length arms. This "super-Y" configuration contained eight buckets and 14 funnel traps for a total of 22 traps. Once opened, arrays were

checked daily. Drift fence array capture data was analyzed by dividing total captures by the total number of trap nights.

Visual encounter surveys (VES) (Crump & Scott, 1994) were conducted at all three sites. Groups of one to six individuals searched a given area and each individual amphibian and reptile observed was recorded. Time spent searching was also recorded. Since the VES had varying numbers of participants and varying search duration, all VES data were transformed to encounters/person hour. Additionally, some species were collected opportunistically. Voucher specimens for each species were collected and have been deposited at the Museum of Zoology at the University of Costa Rica (UCR). Tissue samples were also collected from each species and deposited in the frozen tissue collection at Texas State University, San Marcos, Texas, USA.

Results

Species Composition and Distribution

Overall, 425 individuals comprising 33 species were documented for RNACB including 13 frog, two turtle, nine lizard and nine snake species (Table 10). The most conspicuous species, due to their abundance, proclivity for open spaces and association with human dwellings were *Ctenosaura similis*, *Sceloporus variabilis* and *Ameiva undulata*.

Drift fence arrays were open for 543 trap nights, yielding 127 captures. I captured six frog, three lizard and one snake species in the arrays. The lizard species most captured was *A. undulata* (20 captures) accounting for 15.7% of the total captures

Table 10 Amphibians and reptiles of Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica. Habitat categories: Aqu = aquatic, Arb = arboreal, Bld = manmade structures, Fos = fossorial, Mar = marine, Ter = Terrestrial, Rip = riparian. Diel activity categories: D = diurnal, N = nocturnal, C = crepuscular, ? = unknown

Taxon	Site			Habitat	Diel Activity
	Cabuya	San Miguel	Lagoon		
AMPHIBIANS					
ANURA (13 species)					
Bufonidae (2)					
Bufo coccifer	X		X	Ter	N
Bufo marinus	X	X	X	Ter	N
Leptodactylidae (4)					
Eleutherodactylus fitzingeri	X	X	X	Ter	D/N
Leptodactylus labialis	X	X**		Ter	N
Leptodactylus pentadactylus			X	Ter	N
Leptodactylus poecilochilus		X	X	Ter	N
Hylidae (5)					
Agalychnis callidryas	X	X	X	Arb	N
Hyla microcephala	X		X	Arb	N
Phrynohyas venulosa			X	Arb	N
Scinax boulengeri			X	Arb	N
Smilisca baudinii	X	X	X	Arb	N
Microhylidae (1)					
Hypopachus variolosus	X		X	Fos, Ter	N
Ranidae (1)					
Rana forreri			X	Aqu	N
REPTILES					
TESTUDINATA (2 species)					
Cheloniidae (1)					
Lepidochelys olivacea		X		Mar	?
Kinosternidae (1)					
Kinosternon scorpioides			X	Aqu, Ter	D/N
LACERTILIA (9 species)					
Corytophanidae (1)					
Basiliscus basiliscus	X*			Arb	D

Table 10 continued

Taxon	Site			Habitat	Diel Activity
	Cabuya	San Miguel	Lagoon		
Iguanidae (1)					
Ctenosaura similis	X	X	X	Ter, Arb	D
Phrynosomatidae (2)					
Sceloporus squamosus		X*		Ter	D
Sceloporus variabilis	X	X		Ter, Arb	D
Polychrotidae (1)					
Norops cupreus	X	X	X	Arb	D
Gekkonidae (2)					
Gonatodes albogularis	X	X		Arb, Bld	D
Phyllodactylus tuberculosus	X	X		Bld	N
Scincidae (1)					
Mabuya unimarginata	X	X		Arb	D
Teiidae (1)					
Ameiva undulata	X	X	X	Ter	D
SERPENTES (9 species)					
Boidae (1)					
Boa constrictor		X		Ter, Arb	D/N
Colubridae (8)					
Coniophanes piceivittis			X	Ter?	N?
Leptodeira annulata			X	Arb	N
Leptodrymus pulcherrimus		X		Ter?	D
Leptophis mexicanus			X	Arb	N
Mastigodryas melanolomus	X	X*		Ter	D
Oxybelis fulgidus		X***		Arb	D
Tantilla armillata		X		Ter	D
Trimorphodon biscutatus		X		Ter	D

*=Seen but not vouchered
**=Heard but not vouchered
***=ID from photo

(Table 11). Only two individuals of one snake species, *Coniophanes piceivittis*, were captured, and these were in the lagoon array.

The two arrays near EBSM captured only 13 individuals of two species (*A. undulata* and *Norops cupreus*), whereas the array at the lagoon captured 10 species and 114 individuals, or 89.9% of all captures. Explosive breeding events (23 June 2003, 14-15 August 2003) lead to captures of large numbers of two frog species, *Hypopachus variolosus* (46 captures) and *Phrynohyas venulosa* (32 captures), accounting for 61.4% of all captures (Table 11).

A total of 201.5 person-hours were spent conducting visual encounter surveys. *Eleutherodactylus fitzingeri* (92 observations) and *N. cupreus* (31 observations) were found at all three sites and in all areas of the reserve. Other lizards encountered often in open, sunny areas were *C. similis*, *A. undulata* and *S. variabilis*. I encountered only two snakes more than twice, *Leptophis mexicanus* and *Trimorphodon biscutatus*. All three *L. mexicanus* were in the same tree, whereas the *T. biscutatus* were found at three separate localities.

I encountered the majority of the documented species relatively quickly. Seventeen species were found within three days, and the rate of accumulation slowed considerably after a week (Fig. 6). After 14 days, only 0.26 species/day were added to the collection, and the rate of accumulation decreased to 0.125 species/day by the end of the study.

Table 11 Drift fence array and visual encounter survey capture rates and percentages by species for Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica.

Species	Drift Fence Arrays		Visual Encounter Surveys	
	Number Captured	% of total captures	Number Observed	% of total observed
AMPHIBIANS	**101**	**79.53**	**198**	**66.44**
Anura	**101**	**79.53**	**198**	**66.44**
Bufo coccifer	10	7.87	6	2.01
Bufo marinus	0	0	1	0.34
Eleutherodactylus fitzingeri	6	4.72	92	30.87
Leptodactylus labialis	0	0	3	1.01
Leptodactylus pentadactylus	0	0	1	0.34
Leptodactylus poecilochilus	6	4.72	23	7.72
Agalychnis callidryas	0	0	19	6.38
Hyla microcephala	0	0	11	3.69
Phrynohyas venulosa	32	25.20	7	2.35
Scinax boulengeri	0	0	12	4.03
Smilisca baudinii	1	0.79	14	4.70
Hypopachus variolosus	46	36.22	4	1.34
Rana forreri	0	0	5	1.68
REPTILES	**26**	**20.47**	**100**	**33.56**
Turtles	**0**	**0**	**12**	**4.03**
Kinosternon scorpioides	0	0	12	4.03
Lizards	**24**	**18.90**	**82**	**27.52**
Basiliscus basiliscus	0	0	1	0.34
Ctenosaura similis	1	0.79	20	6.71
Sceloporus variabilis	0	0	19	6.38
Norops cupreus	3	2.36	31	10.40
Gonatodes albogularis	0	0	1	0.34
Phyllodactylus tuberculosus	0	0	0	0
Mabuya unimarginata	0	0	2	0.67
Ameiva undulata	20	15.75	8	2.68
Snakes	**2**	**1.57**	**6**	**2.01**
Boa constrictor	0	0	0	0
Coniophanes piceivittis	2	1.57	0	0
Leptodeira annulata	0	0	2	0.67
Leptodrymus pulcherrimus	0	0	0	0
Leptophis mexicanus	0	0	3	1.01
Mastigodryas melanolomus	0	0	1	.034
Oxybelis fulgidus	0	0	0	0
Tantilla armillata	0	0	0	0
Trimorphodon biscutatus	0	0	0	0

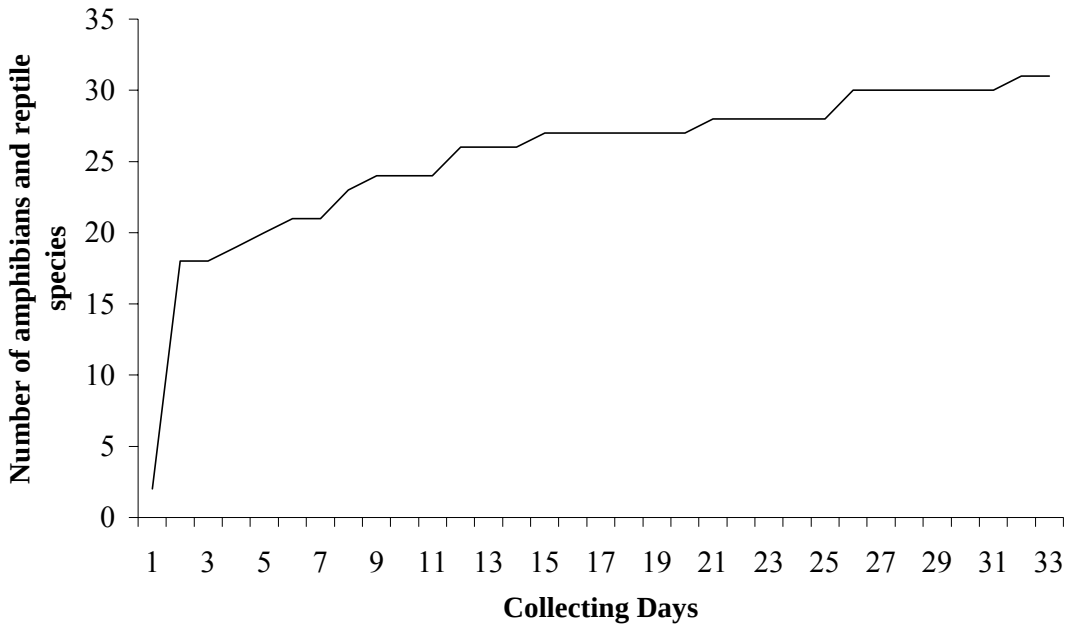

Figure 6 Rate of amphibian and reptile species accumulation at Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica.

Time of Activity

Of the 32 terrestrial species documented at RNACB 40.1% were diurnal, 50% nocturnal, 9.4% were active day and night (Table 10). Trends in activity periods were tied to taxonomic group. All amphibian species were nocturnal, with one, *E. fitzingeri*, also being active in late afternoons. The turtle species, *Kinosternon scorpioides*, was active day and night. Iguanids, skinks and teiids were diurnal, as was the gecko, *Gonatodes albogularis*. However, *Phyllodactylus tuberculosus*, another gecko species, was nocturnal. The snakes, *C. piceivittis*, *L. mexicanus* and *Leptodeira annulata*, all of which feed on anurans, were nocturnal. The remaining six snake species were diurnal except for *B. constrictor*, which is active day and night.

Amphibian Reproduction

Reproductive activity of anurans was observed at all three sites and for all species except *Bufo coccifer*, *Bufo marinus* and *Rana forreri*. *Eleutherodactylus fitzingeri*, a direct developing species, was seen and heard calling throughout the entire reserve.

At ECB, reproductive activity centered on the ephemeral pools found near the station and in the adjacent roads and pastures. I observed *Leptodactylus labialis*, *Smilisca baudinii*, and *Hyla microcephala* calling in chorus, as well as two *Agalychnis callidryas* males calling from a banana plant on the side of the road. Two other species, *Hypopachus variolosus* and *Bufo coccifer* were seen at the ephemeral pools, but were not heard calling at these sites.

At EBSM, reproductive activity was restricted to several pools in a stagnant branch of Quebrada Sam Miguel and the small ephemeral pools in the road to Mal País, north of the station. In the stream pools we found four male *A. callidryas* calling, four egg masses, and tadpoles. On several occasions I heard *S. baudinii* calling along the trail to Mal País and found tadpoles in several tire-rut pools. *Leptodactylus poecilochilus* and *L. labialis* were also heard calling along this road.

The majority of amphibian reproductive activity took place at LB. All documented amphibian species except *L. labialis* were found there, and eight used the lagoon as a breeding site. Different species utilized the lagoon at different times. (Table 12) In early June, when the lagoon was muddy, the foam nesting *L. pentadactylus* and *L. poecilochilus* called from the ground and *A. callidryas* from the trees surrounding the lagoon. Egg masses from the latter were found on leaves overhanging the as of yet dry land. Other species were present, but not calling. By 20 June, the lagoon had expanded to 15 m X 15 m and was several cm deep. With water present, *H. microcephala* began calling and depositing eggs on the long grass above the water. We observed *R. forreri* and *B. coccifer* in the lagoon area, but did not document reproduction for either species.

A downpour of 44 mm on 23 June triggered the season's first explosive breeding event. That night there was a deafening chorus of *S. baudinii*, *P. venulosa*, *and H. variolosus*. Also calling in full chorus were, *H. microcephala*, *A. callidryas* and *L. poecilochilus*. By 0200h, the large chorus of *P. venulosa* and *S. baudinii* had ended; however, *H. variolosus* and *H. microcephala* were still in full chorus and were now joined by *S. boulengeri*, *L. poecilochilus* and the occasional *S. baudinii*.

Table 12 Amphibian calling activity at Laguna Balsitas, Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica.

Date	Full chorus	Sporadically Calling	Present but not calling
7 June, 2003		*A. callidryas* *L. pentadactylus* *L. poecilochilus*	*H. microcephala* *P. venulosa* *S. baudinii*
20 June, 2003	*H. microcephala*	*A. callidryas* *L. pentadactylus* *L. poecilochilus*	*B. coccifer* *P. venulosa* *R. forreri* *S. baudinii*
23 June, 2003 (after heavy rain)	*A. callidryas* *H. microcephala* *H. variolosus* *P. venulosa* *S. baudinii* *S. boulengeri*	*L. pentadactylus* *L. poecilochilus*	
2 August, 2003	*H. microcephala*	*A. callidryas* *L. poecilochilus* *S. boulengeri*	*B. coccifer* *P. venulosa*
17 August, 2003	*H. microcephala*	*A. callidryas* *L. poecilochilus* *S. boulengeri*	*B. coccifer* *H. variolosus* *L. poecilochilus* *P. venulosa* *R. forreri*

Following the rain event of 23 June until the study ended on 17 August, the calling pattern at LB was: *H. microcephala* calling in full chorus each night and *A. callidryas*, *S. boulengeri* and *L. poecilochilus* calling sporadically. *H. variolosus* and *P. venulosa* only called on two other nights, each time after very heavy rain.

Kinosternon scorpioides

Twenty *Kinosternon scorpioides* were collected in the area of the lagoon during the study. Turtles were first noticed on 7 June, in the muddy area of what was to be the lagoon. They were captured from that date forward, first in the mud pit, then in the shallow water and finally along the edge of the filled lagoon. Data taken are summarized in Table 13 and described in the species account below.

Species Accounts

Species accounts are provided below. They include distribution (ECB = Estación Cabuya, EBSM = Estación Biológica San Miguel, LB = Laguna Balsitas) and natural history notes.

Frogs

Agalychnis callidryas (ECB, EBSM, LB)

Previously known only from the LB, this species was present at all three study sites. Near ECB, two individuals were calling on a banana plant on the side of the road. At two stagnant pools at EBSM, several males were heard calling, and four males and two females were found along with four egg masses and tadpoles. The population surrounding the lagoon was large with several dozen males calling each night and dozens of egg masses found on the vegetation surrounding the lagoon.

Bufo coccifer (ECB, LB)

Ten individuals were captured in the LB array and an additional six were observed during the VES. Some were observed in roadside pools near ECB and others were seen around LB. This species was not heard calling.

Bufo marinus (ECB, EBSM)

I observed only three individuals of this species, all around human habitations. None was heard calling within the reserve.

Eleutherodactylus fitzingeri (ECB, EBSM, LB)

The only ubiquitous amphibian species in the reserve, individuals were heard and seen in all areas. Ninety-two individuals were found during VES and an additional six were captured in the drift fence arrays.

Hyla microcephala (ECB, LB)

This species was found along roadside pools at ECB and in LB where it was a persistent caller both nightly and seasonally. Eleven individuals were observed during the VES and a full chorus began continually calling once the lagoon began to fill. Calling continued nightly for the continuation of this study.

Hypopachus variolosus (ECB, LB)

One individual was found near a roadside pool near ECB. I captured 46 individuals in the drift fence array at LB. The majority of these captures occurred on nights following especially heavy rains during mating events.

Leptodactylus labialis (ECB, EBSM)

This species was heard calling in low abundance along the road to ECB and along the road from EBSM to Mal País. This species was not heard calling in the interior of the reserve.

Leptodactylus pentadactylus (LB)

This species was heard calling on three occasions from LB before it filled with water. On 7 June and 20 June, one individual was heard calling all night. On 23 June, three individuals called from the lagoon floor.

Leptodactylus poecilochilus (EBSM, LB)

This species was heard calling along the road from the EBSM to Mal País and at LB. At the lagoon, this species called nightly, from burrows under the mats of tall grass as the lagoon filled, and in lesser numbers once the lagoon was full. This species was not encountered at ECB.

Phrynohyas venulosa (LB)

I only observed this species in and around LB. This large tree frog was seen and heard calling sporadically in the trees surrounding the lagoon. Two explosive reproductive events were documented, on 23 June and 14 August following monsoon rains. Interestingly, the second calling bout occurred in broad daylight, in full sun and 37° C. The calling started before 0950h and continued until 1125h.

Rana forreri (LB)

This species was also found only at LB. Individuals were occasionally seen under a large gourd tree next to the lagoon and in the lagoon itself but none were heard calling. It is possible that this species does not call until later in the rainy season when the lagoon is at maximum capacity.

Scinax boulengeri (LB)

I found this species in the vegetation surrounding the lagoon. Individuals were also observed during the 23 June explosive breeding event. Calling in this species commenced later in the night once *S. baudinii* and *P. venulosa* stopped calling.

Smilisca baudinii (ECB, EBSM, LB)

The most common hylid in the reserve, this species was found at all three localities. At ECB and EBSM, males called in the trees along the roads and tadpoles were present in tire rut pools. At LB, individuals were common in trees surrounding the

lagoon and hundreds were present at the 23 June explosive breeding event. Afterward, they did not call in great numbers at the lagoon.

Turtles

Kinosternon scorpioides (LB)

The only terrestrial turtle species observed, this species was abundant, yet only seen at LB. When only mud was present, turtles were found partially buried in the mud. As the lagoon filled, additional individuals were seen swimming in the water. I captured, measured, marked and released 20 individuals (13♂, 7♀). There were no recaptures. Males on average weighed less and were longer but thinner than females, but none of the differences were statistically significant (Table 13).

Lepidochelys olivacea (Beach)

One dead individual was found washed up on the beach in front of the EBSM dorm.

Lizards

Ameiva undulata (ECB, EBSM, LB)

This teiid was found at all three sites within the reserve. It was abundant along open sunny areas of the trails, at beach margins and near habitations where they actively foraged.

Table 13 Mean ± SD of seven morphological parameters for *Kinosternon scorpioides* found at Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica. All length and width measures are in mm.

Variable	Male (N=13)	Female (N=7)	Total (N=20)	t-statistic	p-value
Straight carapace length	140.2 ± 8.28	135.0 ± 4.20	138.4 ± 7.43	1.5321	0.143
Curved carapace length	166.0 ± 10.10	160.0 ± 7.09	164.0 ± 9.35	1.2988	0.211
Straight carapace width	94.8 ± 4.85	96.2 ± 3.37	95.3 ± 4.34	-0.6450	0.527
Curved carapace width	150.0 ± 6.75	154.0 ± 6.99	152.0 ± 6.89	-1.1483	0.267
Plastron length	128.7 ± 8.16	126.0 ± 7.59	127.7 ± 7.88	0.8163	0.425
Plastron width	73.3 ± 3.47	72.0 ± 2.75	72.8 ± 3.22	0.8422	0.411
Mass (g)	425 ± 51.3	434 ± 36.5	428 ± 45.8	-0.3725	0.714

Basiliscus basiliscus (ECB)

A single large male was observed on Sendero Sueco near ECB, approximately 20 m up a tree. No other individuals were observed.

Ctenosaura similis (ECB, EBSM, LB)

A common lizard in the reserve, *C. similis* was found on the edges of the trails and along the beaches. Juveniles were found near the station buildings and at LB. On 16 August, an adult female was observed capturing and consuming an adult *Sceloporus variabilis*.

Gonatodes albogularis (ECB, EBSM)

I observed several individuals around the buildings at ECB. Additionally, one individual was found at the EBSM. It was found on equipment in the laboratory, therefore it is possible it could have been brought in from elsewhere.

Mabuya unimarginata (ECB, EBSM)

Two individuals of this species were observed: one on a tree in the arboretum next to ECB, and a second on a fence post along the trail from EBSM to Mal País.

Norops cupreus (ECB, EBSM, LB)

The only species of anole found in reserve, *N. cupreus* was common and I found both adults and juveniles throughout the reserve.

Phyllodactylus tuberculosus (ECB, EBSM)

This gecko species was found in habitations at both ECB and EBSM. No individuals of the two introduced geckos (*Hemidactylus frenatus* and *H. garnotii*) were found.

Sceloporus squamosus (ECB)

Dr. James R. Dixon observed individuals of this species along the beach margin at Estación Cabuya (pers. comm.). No individuals were captured however.

Sceloporus variabilis (ECB, EBSM)

One of the more common species, this lizard was found in open sunny areas, along trails, around habitations and on the beach. Hatchlings of this species were seen during the later part of the survey at RNACB.

Snakes

Boa constrictor (EBSM)

One individual was found dead on the trail from the EBSM to Mal País. The cause of death was unknown, but the snake was severely emaciated. A second individual was observed by a park guard near the dorm at EBSM, but was not captured.

Coniophanes piceivittis (LB)

Two individuals were captured in a funnel trap of the drift fence array located adjacent to LB. Both were captured on the lagoon side of the array. It is possible that they were foraging for frogs when trapped.

Leptodeira annulata (LB)

Two individuals were found along the Sendero Central south of Laguna Balsitas. The first was a juvenile found coiled in the branches of a fallen tree, the second an adult found on the ground near the beach.

Leptodrymus pulcherrimus (EBSM)

The lone individual of this species captured was found crawling out from under the EBSM main house.

Leptophis mexicanus (LB)

Three juveniles were found on branches of the same tree on the edge of Laguna Balsitas. Several *A. callidryas* adults and eggs masses were found on the tree where the snakes were collected.

Mastigodryas melanolomus (ECB, EBSM)

This species seems to be distributed throughout the reserve. I captured an individual near ECB on Sendero Danes and observed another near the lab at EBSM.

Oxybelis fulgidus (EBSM)

I did not directly observe this species. It was identified from a photograph provided by Dr. Erin S. Lindquist. The snake was photographed outside of the laboratory at EBSM.

Tantilla armillata (EBSM)

A single hatchling (SVL = 98 mm) was found on a tree stump outside of the laboratory at EBSM.

Trimorphodon biscutatus (EBSM)

Three individuals were found, at or near EBSM making this species the most encountered snake.

Discussion

As the first collecting effort of any magnitude at the RNACB and in the lower Nicoya Peninsula, this study takes a first step in identifying the distribution of amphibians and reptiles in the region. Of the 32 species observed, 22 were collected for the first time on the lower Nicoya Peninsula. This locality represents the southernmost extension of the range for seven of those 22 species: *P. tuberculosus, S. variabilis, A. undulata, C. piceivittis, L. mexicanus, O. fulgidus,* and *T. biscutatus*.

How complete is the inventory at RNACB? Lack of prior collecting effort in the region made it difficult to assess what species may be present, but that I did not collect.

A review of the range maps in Savage (2002) revealed few historical collecting localities on the Nicoya peninsula, nor were there records of additional species in the Museum of Zoology at the University of Costa Rica. The lower half of the peninsula has been very poorly surveyed. Only 15 species were previously collected in the vicinity of the reserve, and I captured all but four of those in this study (Table 14). While I clearly did not capture all of the species present, the relatively flat accumulation curve indicates substantial effort would be needed to detect additional species. Using the accumulation rate of 0.125 species/day, it would take an additional 40 days to find the five undetected species known to occur in the vicinity.

Traditional local knowledge may give insight into encounter probabilities of rare species (Berkes, 1999; Laird, 2002), and completeness of herpetological inventories. I interviewed Don Carlos, Costa Rica's first park guard (Guardaparque), who has worked in the reserve since its creation in 1963. Don Carlos identified ten species from photographs, mostly snakes, that were not collected (Table 14). Interestingly, some were very rarely encountered; for example, only one individual of the easy to identify *Crotalus durrisus* was seen in 42 years. Hence, many species may be much less likely to detect than reflected by the species accumulation rate.

As a whole, the reserve's species assemblage is similar to those of the nearby dry forest sites to the north; however, species richness is not as high in RNACB. The RNACB has 45 species likely to be present (using traditional knowledge combined with our data), compared to 78 at Parque Nacional Santa Rosa. The difference in species richness is due in great part to the presence of more species from families shared among

Table 14 Species not encountered in this study that have been documented or are possible for Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica. Documentation includes voucher specimens, literature review and interview with long time RNACB personnel.

Species	Voucher	Visual	Source
Amphibians			
Bufo luetkenii	X		Savage 2002
Reptiles			
Rhinoclemmys pulcherrima	X		Savage, 2002
Gymnopthalmus speciosus	X		Savage, 2002
Iguana iguana		X	Don Carlos, (pers. comm.)
Clelia clelia		X	Don Carlos, (pers. comm.)
Drymobius margaritiferus		X	Don Carlos, (pers. comm.)
Elaphe triaspis	X		Savage, 2002
Imantodes sp.		X	Don Carlos, (pers. comm.)
Oxybelis aeneus		X	Don Carlos, (pers. comm.)
Spilotes pullatus		X	Don Carlos, (pers. comm.)
Micrurus nigrocinctus		X	Don Carlos, (pers. comm.)
Crotalus durrisus		X	Don Carlos, (pers. comm.)
Porthidium ophryomegas		X	Don Carlos, (pers. comm.)

the two sites. For example, more species of colubrid snakes are known from PNSR than RNACB. However, seven families absent from RNACB are represented by one species at PNSR. These include Caeciliidae, Rhinophrynidae, Corytophanidae, Leptotyphlopidae, Loxocemidae, Elapidae and Crocodylidae.

Palo Verde National Park, located near RNACB at the southern portion of the base of the Nicoya Peninsula, has 38 species verified with voucher specimens at the Natural History at the University of Costa Rica. This number however, undoubtedly underestimates the number of species present in the park, making comparisons difficult. This lack of documented species at Palo Verde and indeed along the entire Nicoya Peninsula precludes identification of a gradient in species richness that could be attributed to peninsula effects (Simpson, 1964; Seib, 1980; Busack & Hedges, 1984; Means & Simberloff, 1987).

Explosive anuran breeding events, for example what I experienced with *H. variolosus* and *P. venulosa*, strongly influenced capture rates. With captures from explosive breeding events removed, the capture rate dropped from 0.234 to 0.109 captures/trap night. The latter rate may reflect the non-breeding detectability of some amphibian species. Taken together, the data show the stochastic nature of detectability of numbers of amphibians in tropical settings.

Available oviposition sites and rainfall dictated amphibian reproduction at RNACB. Reproductive activity at Cabuya and EBSM were limited to ephemeral pools and one temporary river pool and only the direct developing *Eleutherodactylus fitzingeri* called throughout the reserve. The majority of the reproductive activity however,

occurred at Laguna Balsitas. Not surprisingly, the anuran community at LB separated their reproductive activities in space and time. Much of the observed reproductive activity was consistent with published accounts. Foam nesting Leptodactylid frogs are known to call as temporary bodies of water fill (Savage, 2002). Three species (*Smilisca baudinii*, *Phrynohyas venulosa, Hypopachus variolosus*) observed in explosive breeding events have been associated with these events (Duellman, 2001; Savage, 2002). Furthermore, the toad *B. coccifer,* not heard calling, has been documented to not call for months after arriving at a breeding site (Savage, 2002). With continued monitoring *B. coccifer* (and *R. forreri*) would have likely been heard calling later in the wet season.

Little information exists on anuran reproductive communities in Costa Rica. The one exception is Donnelly & Guyer's (1994) work on Hylid reproduction at La Selva. Although their site was on the Caribbean versant and contained a different anuran assemblage, notable similarities exist. As was the case at La Selva, *A. callidryas* called from higher perches than other species and deposited eggs over dry land in anticipation of water. The explosive breeders at both sites were most common early in the wet season and like La Selva, LB had two species of prolonged breeders, though in the case of LB *H. microcephala* and not *H. ebraccata* joined *A. callidryas* as one of these species. Donnelly & Guyer (1994) also documented anuran predation by several colubrid snakes at La Selva. Similarly, it is likely that the three *L. mexicanus* found at LB were predating on *A. callidryas* adults or egg masses. A longer study of anuran reproduction at Laguna Balsitas is needed to make rigorous comparisons, but utilizing observations made in this study, one can hypothesize that, like La Selva, RNACB has seasonal anuran

reproduction, and that habitat use, phenology, reproductive strategy and predation play a role in structuring the anuran community.

The aggregation of *K. scorpioides* at the filling lagoon is consistent with behavior at other sites in Costa Rica (Acuña Mesén, 1990; Acuña Mesén, 1998). Interestingly though, *K. scorpioides* at RNACB are smaller than elsewhere in the country. Acuña Mesen (1992) provides the following range for SCL (95 – 185 mm; $\overline{X}$ = 156.9 mm) and CCL (134 – 210 mm; $\overline{X}$ = 184.9 mm) for *K. scorpioides* in Costa Rica. Additionally, morphometric data are available for three Costa Rican *K. scorpioides* populations (Acuña Mesén, 1990; Acuña Mesén, 1992; Marquez, 1995). The Cabo Blanco population is smaller in mean size (SCL, CCL and/or weight), than all other Costa Rican populations and the national means. This holds for the population as a whole as well as males and females separately.

In addition to providing a list of herps for RNACB, this study provides a baseline for future biodiversity assessments that include herpetofauna on the Nicoya Peninsula. Continual accrual of biodiversity information will enable us to better understand species distributions and provide raw material for hypothesis testing about the biogeography of Mesoamerican herpetofauna. Furthermore, it demonstrates the importance of Cabo Blanco as a site for future studies of anuran reproduction, chelonian communities and the dynamics of neotropical amphibian and reptile communities.

CHAPTER VI

ENVIRONMENTAL CORRELATES TO HERPETOFAUNAL DIVERSITY IN COSTA RICA

Synopsis

Understanding processes that underlie current patterns of species diversity continues to be a major goal of ecology. It has been shown that factors that influence species distributions become important at different temporal and special scales. At the regional scale, species diversity patterns can best be described in terms of three diversity components (alpha, beta and gamma). In this study, I used amphibian and reptile assemblages at 17 sites, distributed within and among major ecoregions in Costa Rica, to discover regional level species diversity patterns and elucidate their causes. Amphibian alpha diversity was highest in lowland Pacific rainforests and reptile alpha diversity was highest in lowland Atlantic rainforests. Tropical dry forests and the high elevation site contained low alpha diversity but contributed greatly to the region's beta diversity. Beta diversity was lowest among the three lowland regions (tropical dry forest, lowland Atlantic rainforest, lowland Pacific rainforest) and highest between the highland site and all others. Two climate gradients were important in determining the observed species diversity at sites. An elevation/temperature gradient separated high and mid elevation sites from lowland sites, and a sun/rain gradient was important in the formation of lowland site patterns. The elevation/temperature gradient was most correlated to reptile diversity and the sun/rain gradient was most correlated to amphibian diversity. By

protecting sites among and between regions, and therefore both alpha and beta diversity, the system of protected areas in Costa Rica is doing a good job of conserving the country's overall herpetofaunal diversity. However, ongoing changes to the global climate have the potential to affect these patterns and should be studied.

Introduction

Disentangling the factors that determine patterns of species diversity remains a central theme of ecology and is fundamental to understanding processes that govern ecological communities as well as designing appropriate conservation strategies for those communities (MacArthur, 1965; Schiebe, 1987; Ricklefs & Schluter, 1993a). This understanding becomes increasingly important in light of current rates of habitat destruction and fragmentation, which have created the current biodiversity 'crisis' (Soulé, 1986; Raven & Wilson, 1992). Although universal rules governing the arrangement of biodiversity remain elusive, ample literature exists describing the interplay between historical, regional, and local processes in the formation of present-day patterns of species diversity (MacArthur & MacArthur, 1961; Pianka, 1966a, b; Terbourgh, 1973; Ricklefs & Schluter, 1993a; Rozenswieg, 1995; Brown & Lomolino, 1998). However, the roles of historical and local factors vary according to taxon group and geographic setting, and the contributions of each are not equal at all spatial scales (Scott *et al.*, 2002).

At the regional scale, species diversity (γ-diversity) is a consequence of within-community diversity at all sites (α-diversity) plus the similarities and differences in diversity among sites (β-diversity) (Loreau, 2000). As such, comparisons of α and β

diversity coupled with information about topographic features, rainfall, seasonality, and habitat affinities of species, allow us to infer causes of diversity at the regional and local scales.

The diversity of herpetofauna in Costa Rica provides an excellent model for studying correlates of species diversity. A small country (50,900 km²), roughly the size of West Virginia, USA, Costa Rica contains close to 4% of the earth's total biodiversity (Vargas Ulate, 1992). This high diversity is reflected in its herpetofauna, which consists of 174 amphibian and 222 reptile species (Leenders, 2001; Savage, 2002). These species are distributed across a varied landscape that includes many climatic regimes, life zones, and elevations. Furthermore, the country has protected approximately twenty five percent of its land (Evans, 1999) and has encouraged biological study, providing the necessary data to analyze diversity at multiple scales.

Previous work on herpetofaunal diversity of Costa Rica focused mainly on studying diversity from the top down; that is, understanding the historical biogeographic patterns that have led to the regional species pools on the Pacific and Atlantic versants (Savage, 1966, 1982, 2002). In his seminal work on the subject, Savage (1966, 1982, 2002) described historical vicariance and dispersal events that produced the present day Central American amphibian and reptile species pool. These historical factors constrained the regional species pool of snakes, for example, by limiting which clades are present in a region (Cadle & Greene, 1993). As a result of his analyses, Savage (2002) divided the country into five "discrete recognizable [herpeto]faunal areas" each with a separate history. They are: Lowland Pacific Northwest; Lowland Southwest;

Lowland Atlantic; and Upland/Highland-Montane slopes-Cordillera Central; and Cordillera de Talamanca Highland. Although of great importance in understanding the global pattern of amphibian and reptiles diversity in Costa Rica, historical analysis of the species pool only goes so far toward explaining differences in species assemblages at multiple sites.

The purpose of this study is to fill a gap in the understanding of Costa Rican herpetofaunal diversity by taking a bottom-up approach to understanding regional diversity. I compared alpha and beta diversity at 17 sites throughout the country, and tested for associations among abiotic environmental correlates and observed patterns. I used a multivariate analysis to assess the relationship between species distributions in Costa Rica and the combination of environmental variables that exist throughout the country. I predicted that climate variables relating to energy and moisture, as well as topography, would explain species turnover among sites (beta diversity). Sites within similar habitats should have low beta diversity, and beta diversity should be high among sites with distinct habitats. With an understanding of historical constraints on the regional species pool (sensu Cadle & Greene, 1993), I predicted climatic variables would be associated with presence and absence of clades at individual sites. Additionally, I used the assembled species diversity data sets to test Savage's delineation of herpetofaunal regions. I expected sites within each herpetofaunal region to have lower beta diversity values than sites located in other regions. Finally, I discuss the conservation implications of observed amphibian and reptile species richness patterns in

Costa Rica, and discuss the implications of continued global climate change on those patterns.

Methods

Data Sources

I used literature, the specimen database at the natural history museum of the University of Costa Rica (UCR), and three field surveys (Chapters I, II and III) to compile lists of amphibian and reptile species from 17 sites (Fig. 7, Tables 15 and 16). I followed taxonomic designations in Savage (2002), O'Neill & Mendelson III (2004) and Savage & Wake (2001). Sites were selected to include major habitat types while allowing for replication within major ecoregions. Three sites were tropical dry forest (TDF), four were lowland rainforest on the Atlantic versant (LA), three were lowland Pacific rainforest (LP), four were mid elevation sites (ME), and one, Cerro de la Muerte (CM), was a high altitude site. Additionally, two sites (Carara, Cabo Blanco) were located along the transitional Central Pacific Coast. Chapter I illustrated that Carara, though a transitional site, most closely resembles the herpetofauna of the country's wet lowland Pacific forest, although it also contains tropical dry forest species. Conversely, Reserva Natural Absoluta Cabo Blanco, located at the tip of the Nicoya Peninsula in Northwest Costa Rica, has been shown to contain a tropical dry forest herpetofaunal assemblage (Chapter III). For these reasons, Carara is treated as a lowland pacific site and Cabo Blanco as a tropical dry forest.

Environmental data (Table 17) were acquired from the Atlas Climatológico de Costa Rica (Barrantes, 1985) and Clima de Costa Rica (Gomez, 1986). Additionally,

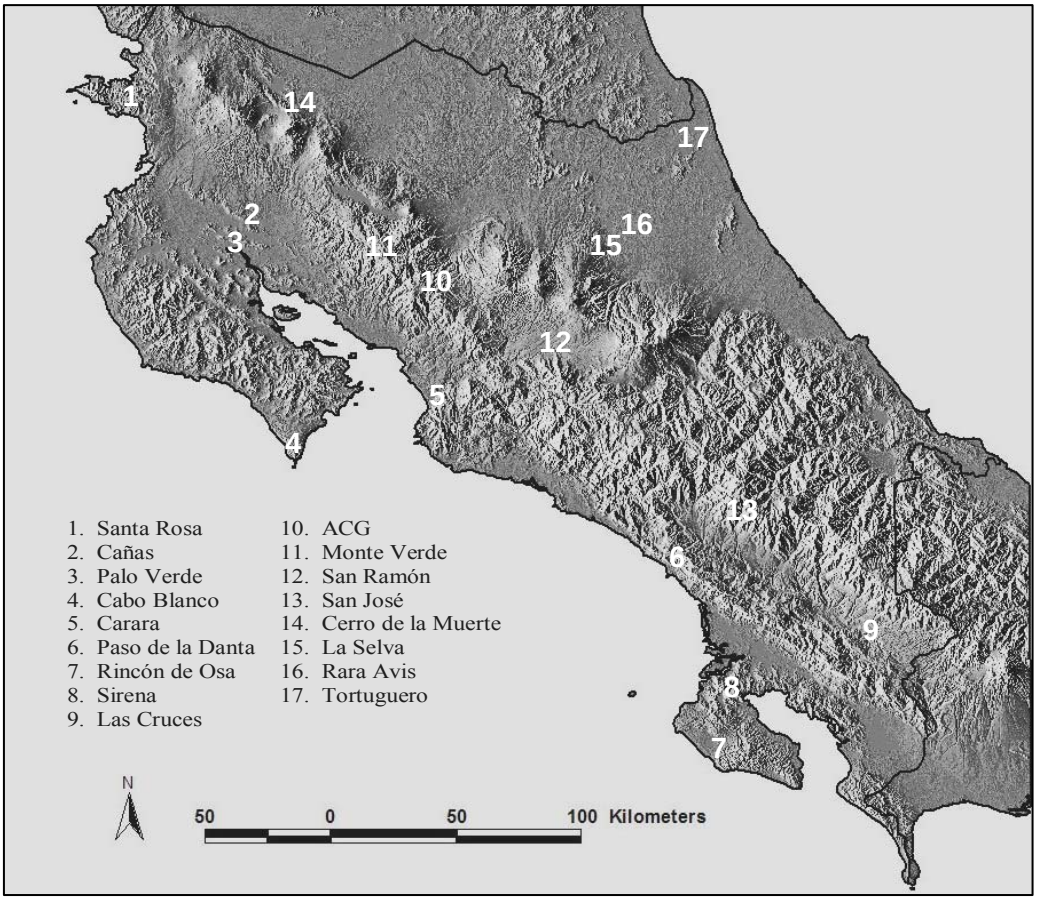

Figure 7 Map of Costa Rica showing 17 surveyed sites.

Table 15 Amphibian alpha diversity for 17 localities in Costa Rica. Sources of data are provided.

	Gymnophiona	Caudata	Anura	**Amphibia**	**Source**
Santa Rosa	1	0	17	18	Sasa & Solórzano, 1995
Cañas	1	0	22	23	Scott *et al.,* 1983
Palo Verde	0	0	11	11	UCR Museum of Natural History
Cabo Blanco	0	0	14	14	Chapter III
Carara	1	3	37	41	Chapter I
Paso de la Danta	2	3	45	50	Ryan, (pers. comm.)
La Sirena	2	3	31	36	McDiarmid & Savage, 2005
Rincón de Osa	1	4	41	46	McDiarmid & Savage, 2005
Las Cruces	4	4	42	50	Scott *et al.,* 1983
San Ramon	0	1	29	30	Bolaños & Ehmcke, 1996
Monteverde	1	5	33	39	Hayes *et al.,* 1984
San José	2	3	12	17	Scott *et al.,* 1983
Cerro de la Muerte	1	3	5	9	Scott *et al.,* 1983
ACG	1	1	30	32	Chapter II
La Selva	1	3	45	49	Donnelly, 1994; Guyer, 1994
Rara Avis	2	2	35	39	Leenders, (pers. comm.)
Tortuguero	1	2	33	36	Burger, 2001

Table 16 Reptile alpha diversity for 17 localities in Costa Rica. Sources of data are provided.

	Crocodylia	Testudinata	Sauria	Serpentes	**Reptilia**	**Source**
Santa Rosa	1	2	18	33	54	Sasa & Solórzano, 1995
Cañas	2	3	16	34	55	Scott *et al.,* 1983
Palo Verde	1	2	6	18	27	UCR Museum of Natural History
Cabo Blanco	0	2	9	10	21	Chapter III
Carara	1	2	24	37	64	Chapter I
Paso de la Danta	2	5	30	40	77	Ryan, (pers. comm.)
La Sirena	1	3	21	33	58	McDiarmid & Savage, 2005
Rincón de Osa	2	3	22	42	69	McDiarmid & Savage, 2005
Las Cruces	0	0	20	39	59	Scott *et al.,* 1983
San Ramon	0	0	18	23	41	Bolaños & Ehmcke, 1996
Monteverde	0	0	12	45	57	Hayes *et al.,* 1984
San José	0	3	3	13	19	Scott *et al.,* 1983
Cerro de la Muerte	0	0	2	6	8	Scott *et al.,* 1983
ACG	0	2	16	23	41	Chapter II
La Selva	2	5	25	57	89	Donnelly, 1994; Guyer, 1994
Rara Avis	0	3	22	48	73	Leenders, (pers. comm.)
Tortuguero	2	5	27	41	75	Burger, 2001

Table 17 List of environmental variables used in Canonical Correspondence Analysis.

Elevation	Annual mean daily sunlight hours
Mean temperature	March mean daily sunlight hours
Max temperature	August mean daily sunlight hours
Min temperature	Insolation
Yearly precipitation	Number of dry months
Dry season precipitation	Potential evapotranspiration (PET)
Wet season precipitation	

monthly mean rainfall values from Barrantes (1985) were summed to derive dry (January- March) and wet (April-December) season rainfall totals for each site.

Analyses

Amphibian and reptile data were analyzed separately. Marine and introduced species were not considered, and species recently presumed extinct were not omitted from the analysis. Alpha diversity was the species richness at each site. Beta diversity was measured using Jaccard's Similarity Index (JSI):

$$JSI = \frac{C}{C + N_1 + N_2}$$

where C = species found in both sites, N_1 = species found in site one but not two, N_2 = those found in site two but not one. The JSI values were used in a cluster analysis with the UPGMA (unweighted pair-group-method-using-arithmetic-averages) option. This method produced clusters of similar species assemblages (low Beta diversity), which were visualized with dendrograms (Sneath & Sokal, 1973; McGarigal *et al.,* 2000).

I used Canonical Correspondence Analysis (CCA) in program CANOCO 4.5 (Ter Braak & Smilauer, 2002) to analyze the influence of environmental variables on patterns of species diversity among the sites. CCA is a direct gradient analysis in which the site and species distributions are constrained by the environmental variables. Due to multicollinearity among environmental variables, a reduced set of five variables (Elevation, Mean Annual Sunlight Hours, Mean Annual Precipitation, Insolation, Dry Months) was used for the CCA analysis with the forward manual selection option to include only significant variables. The significance of each factor was computed with a

Monte Carlo test (9999 permutations), and only factors with $p < 0.05$ were retained. Separate CCAs were run for amphibians, reptiles, and each order.

Results

Amphibians

Alpha Diversity

One hundred twenty-eight amphibian species from 10 families were documented in this study, representing 71.1% of Costa Rican amphibian species (Table 15). Amphibian alpha diversity values ranged from nine species at Cerro de la Muerte to 50 at Paso de la Danta and Las Cruces, with a mean of 31.8 species/site (N = 17, s.d. = 14.02). Anurans made up the majority (> 70%) of amphibian species at all sites except for CM (40%), which was characterized by higher caecilian and salamander diversity.

Lowland Pacific sites contained the highest mean amphibian species diversity ($\overline{X}$ = 43.3, n = 4, s.d = 6.08), whereas the highland site, Cerro de la Muerte, had the fewest (N = 9). Tropical dry forest sites averaged 16.5 amphibian species (n = 4, s.d = 5.20). Mean alpha diversity of caecilians was highest at ME sites ($\overline{X}$ = 1.75, n = 4, s.d = 1.71) and lowest in the TDF ($\overline{X}$ = 0.5, n = 4, s.d = 0.58). Salamanders were altogether absent from TDF sites, and their mean alpha diversity peaked in the ME ($\overline{X}$ = 3.25, n = 4, s.d = 1.71) and LP sites ($\overline{X}$ = 3.25, n = 4, s.d = 0.50). Mean anuran alpha diversity was highest in the LP region ($\overline{X}$ = 38.5, n = 4, s.d = 5.97) and was lowest at CM (N = 5) and in the TDF ($\overline{X}$ = 16, n = 4, s.d = 4.69).

The percentage of amphibians in the overall herpetofauna increases with elevation. It is lowest in the dry forest (29.6%) increases in lowland rainforest sites (Pacific = 39.2%, Atlantic = 35.9%) increases further in ME sites (43.6%) and peaks at CM (52.9%). Families that contributed most to amphibian alpha diversity were: Leptodactylidae (between 8.3-60.0% of total anuran alpha diversity) and Hylidae (between 20.0-36.7% of total anuran alpha diversity). Two families, Centrolenidae and Dendrobatidae, were not represented in TDF sites while one family, Rhinophrynidae, was restricted to three of the dry forest sites.

Beta Diversity

JSI values for amphibians (Table 18) ranged from zero between Cerro de la Muerte and several sites to 0.783 between Parque Nacional Santa Rosa and Cañas. The dendrogram based on amphibian JSI values illustrate the patterns in beta diversity (Fig. 8). High JSI values cluster three distinct groups of sites. Not surprisingly, this low beta diversity corresponds to the three lowland faunal areas (LP, AP, TDF). This grouping reflects the sharing of a high number of species between sites within the same ecoregion. Beta diversity was high among mid elevation sites and between regions. Interestingly, Las Cruces, a mid elevation site clustered with the LP sites (although at a low similarity) and not with the other ME sites. The TDF sites and highland site, CM, were the most distinct clusters. Among lowland groups, the dry forest cluster was the least similar to the other lowland clusters. When amphibians were analyzed at the level of taxonomic Order, the same three clusters (LP, LA, TDF) were produced in Caudata and Anura but not in Gymnophiona.

Table 18 Amphibian similarity among 17 surveyed sites in Costa Rica. The number of shared species between sites are above the diagonal and Jaccard's Similarity index values are below.

	St Rosa	Cañas	PVerde	Cabo	Carara	Danta	Cruces	Sirena	Rincon	ACG	SnRamon	MtVerde	SnJose	Cerro	LaSelva	RAvis	Tortug
StRosa	—	18	11	12	13	10	8	4	7	9	1	5	4	1	7	6	8
Cañas	0.783	—	11	13	17	14	11	8	11	11	2	6	5	1	10	9	11
PVerde	0.611	0.478	—	7	7	6	4	2	4	6	0	2	2	0	3	3	3
Cabo	0.600	0.542	0.389	—	13	9	5	6	7	8	1	5	4	1	6	6	7
Carara	0.283	0.362	0.156	0.310	—	34	21	26	31	17	10	11	8	2	22	17	17
Danta	0.172	0.237	0.109	0.164	0.596	—	28	34	43	18	12	13	6	0	25	20	17
Cruces	0.133	0.177	0.070	0.085	0.300	0.389	—	15	25	13	15	18	11	2	21	21	16
Sirena	0.080	0.157	0.044	0.136	0.510	0.654	0.211	—	35	10	7	5	3	0	16	12	12
Rincon	0.123	0.190	0.075	0.132	0.554	0.811	0.352	0.745	—	12	10	9	5	0	23	18	15
ACG	0.220	0.250	0.162	0.211	0.304	0.281	0.188	0.172	0.182	—	10	10	4	1	24	22	22
SnRamon	0.021	0.039	0.000	0.023	0.164	0.176	0.231	0.119	0.152	0.192	—	15	4	2	18	15	11
MtVerde	0.096	0.107	0.042	0.104	0.159	0.171	0.254	0.071	0.118	0.164	0.278	—	12	3	12	13	10
SnJose	0.129	0.143	0.077	0.148	0.160	0.098	0.196	0.060	0.086	0.089	0.093	0.273	—	3	6	7	6
Cerro	0.038	0.032	0.000	0.045	0.042	0.000	0.035	0.000	0.000	0.025	0.054	0.067	0.130	—	0	1	0
LaSelva	0.117	0.161	0.053	0.105	0.324	0.338	0.269	0.232	0.319	0.421	0.295	0.158	0.100	0.000	—	30	33
RAvis	0.118	0.170	0.064	0.128	0.270	0.290	0.309	0.190	0.269	0.449	0.278	0.200	0.143	0.021	0.517	—	27
Tortug	0.174	0.229	0.068	0.163	0.283	0.246	0.229	0.200	0.224	0.478	0.200	0.154	0.128	0.000	0.635	0.563	—

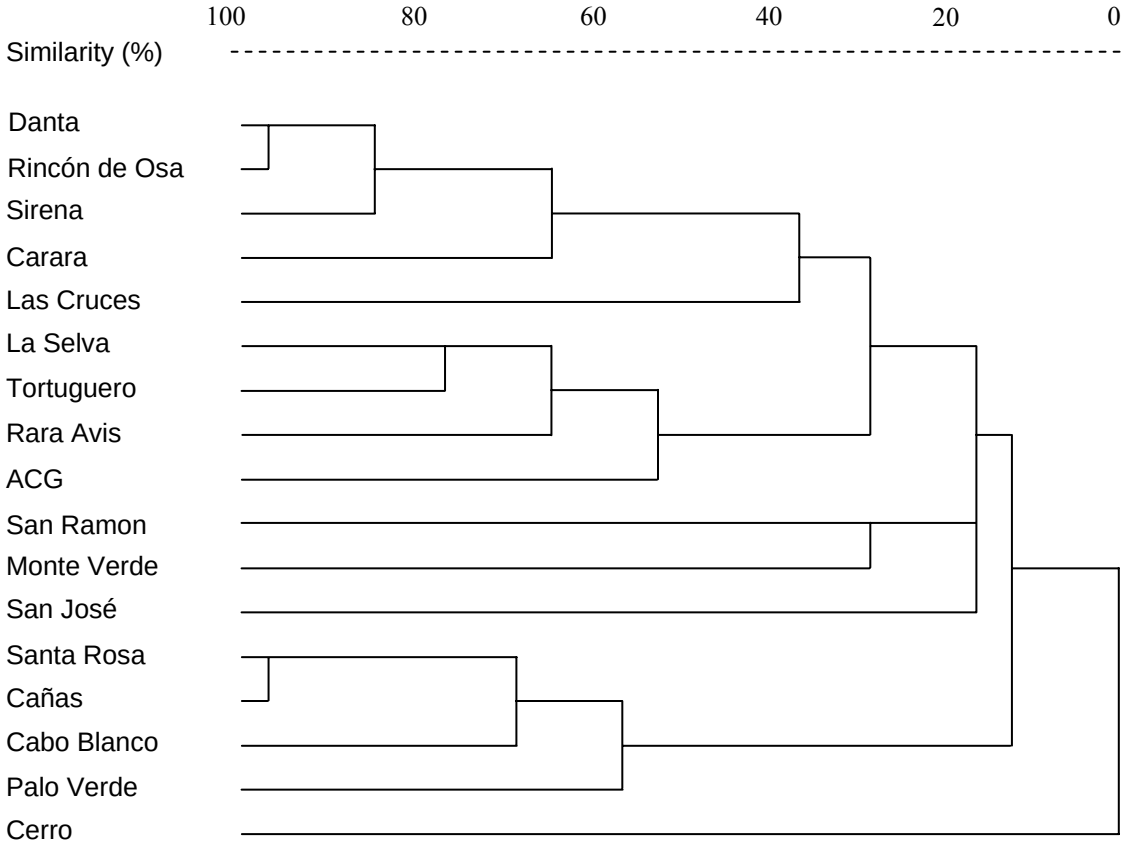

Figure 8 Amphibian dendrogram based on Jaccard's Similarity Index values (percent) for 17 Costa Rican sites. Clustering is based on UPGMA method. Site abbreviations are Paso la Danta (La Danta); Área de Conservación Guanacaste (ACG); Cerro de la Muerte (Cerro).

Environmental Correlates

The amphibian CCA distributed the 17 localities along two primary environmental gradients that explained 29.8% of the variance in the data (Fig. 9). Axis one explained 17.2% of the variation and was positively related to elevation. Axis two explained an additional 12.6% of the variance and described a gradient of insolation and annual mean daily sunlight hours that corresponded to amphibian diversity across the sites. The pattern reflected in the CCA supported the results of the cluster analysis. In a CCA ordination space, proximity of sites along the axes equates to similarity between two sites based on environmental conditions, whereas the cluster analysis was based on JSI values. As in the cluster analysis lowland sites in the same regions were similar. Mid elevation sites grouped loosely near each other, and the one high elevation site (Cerro de la Muerte) was distinct. Northwest dry forest sites were negatively associated with axis one and positively with axis two, corresponding to sites in lowland hot sunny areas with little rainfall. The Pacific lowland sites were negatively related to axis one and somewhat positively related to axis two. Atlantic lowland sites were primarily negatively related to axis two. The mid elevation sites were positively related to axis one and Cerro de la Muerte was highly related to axis one.

Reptiles

Alpha Diversity

A total of 188 reptile species in 24 families were documented, representing 90% of all Costa Rican reptile species (Table 16). Reptile alpha diversity values ranged from

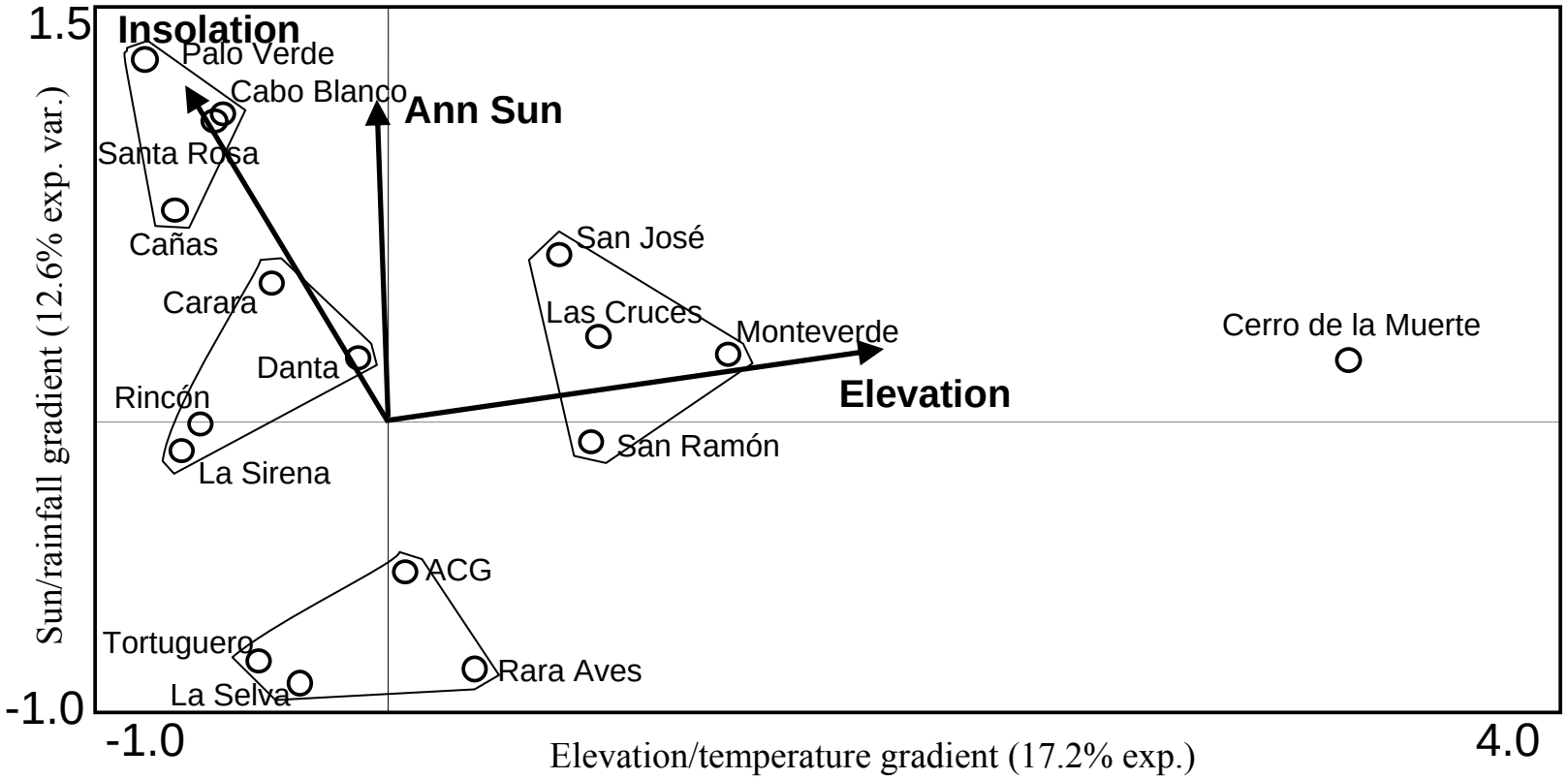

Figure 9 Results of amphibian canonical correspondence analysis for 17 sites in Costa Rica. The relative importance of each environmental variable is indicated by the length of the arrow. Percentage of variation explained by each axis is provided in the parentheses. Abbreviations are as follows: Annual Mean Daily Sunlight Hours (Ann Sun); Área de Conservación Guanacaste (ACG); Paso de la Danta (Danta); Rincón de Osa (Rincón).

eight at Cerro de la Muerte to 89 at La Selva, with a mean of 51.2 species/site (N = 17, s.d. = 22.88). Snakes constituted the majority of reptile species present at all sites. Overall reptile alpha diversity was highest in the LA ($\overline{X}$ = 69.5, n = 4, s.d. = 20.29) and lowest for Cerro de la Muerte (N = 8) and the TDF ($\overline{X}$ = 39.3, n = 4, s.d. = 17.78). Among reptile orders, alpha diversity patterns varied. Crocodilians and, to a lesser extent, turtles were restricted to lowland sites. The greatest turtle diversity was in the LA ($\overline{X}$ = 3.8, n = 4, s.d. = 1.50). Lizard alpha diversity was highest in the LP sites ($\overline{X}$ = 24.3, n = 4, s.d = 4.03) and low at CM (N = 2) and the TDF ($\overline{X}$ = 12.3, n = 4, s.d. = 5.68). Snake alpha diversity was greatest in the LA ($\overline{X}$ = 42.3, n = 4, s.d. = 14.41) and lowest at CM (N=6) and in the TDF ($\overline{X}$ = 23.8, n = 4, s.d. = 11.73). The families that contributed most to reptile alpha diversity were Polychrotidae (between 4.04-10.5% of total lizard alpha diversity) and Colubridae (between 27.2-34.1% of total snake alpha diversity).

Beta Diversity

Reptile JSI values ranged from zero between Cerro de la Muerte and several sites to 0.787 between PNSR and Cañas (Table 19). As with amphibians, low beta diversity within lowland faunal areas produced clusters of LP, LA and TDF sites (Fig. 10). Dry forest sites once again were most dissimilar among lowland groups and the LP and LA groups clustered together. Mid elevation sites had low similarity values and did not cluster into a defined group. Cerro de la Muerte is greatly dissimilar to all other sites and groups. Similar patterns emerged when reptile orders were analyzed separately, albeit with exceptions. For example, the turtle dendrogram grouped Carara

Table 19 Reptile similarity among 17 surveyed sites in Costa Rica. Numbers above the diagonal are number of shared species between sites and numbers below the diagonal are Jaccard's Similarity index values.

	StRosa	Cañas	PVerde	Cabo	Carara	Danta	Cruces	Sirena	Rincon	ACG	SnRamon	MtVerde	SnJose	Cerro	LaSelva	RAvis	Tortug
StRosa	—	48	24	20	24	17	6	11	12	8	4	17	6	1	17	11	17
Cañas	0.787	—	27	20	23	21	7	14	15	8	4	19	7	1	20	12	20
PVerde	0.421	0.491	—	12	10	11	2	7	8	2	1	8	6	0	9	5	10
Cabo	0.364	0.357	0.333	—	11	10	3	6	5	3	1	9	5	0	6	3	8
Carara	0.255	0.240	0.123	0.149	—	48	27	41	41	23	18	18	9	1	44	34	36
Danta	0.149	0.189	0.118	0.114	0.516	—	33	50	55	28	20	15	10	0	53	41	47
Cruces	0.056	0.065	0.024	0.039	0.281	0.320	—	28	34	20	25	22	6	2	37	37	24
Sirena	0.109	0.141	0.090	0.082	0.506	0.588	0.315	—	53	23	15	14	5	0	40	32	34
Rincon	0.108	0.138	0.091	0.059	0.446	0.604	0.362	0.716	—	25	19	18	5	1	46	36	37
ACG	0.092	0.091	0.030	0.051	0.280	0.311	0.250	0.303	0.294	—	18	13	4	0	39	33	35
SnRamon	0.044	0.043	0.015	0.016	0.207	0.204	0.333	0.179	0.209	0.281	—	14	3	2	27	28	22
MtVerde	0.181	0.204	0.105	0.130	0.175	0.126	0.234	0.139	0.167	0.153	0.167	—	11	6	25	21	19
SnJose	0.090	0.104	0.150	0.143	0.122	0.116	0.083	0.069	0.060	0.071	0.053	0.169	—	1	9	8	6
Cerro	0.016	0.016	0.000	0.000	0.014	0.000	0.031	0.000	0.013	0.000	0.043	0.102	0.038	—	2	1	0
LaSelva	0.135	0.161	0.084	0.058	0.404	0.469	0.333	0.374	0.411	0.429	0.262	0.207	0.091	0.021	—	64	68
RAvis	0.095	0.103	0.053	0.033	0.330	0.376	0.389	0.323	0.340	0.407	0.326	0.193	0.095	0.013	0.653	—	51
Tortug	0.152	0.182	0.109	0.091	0.350	0.448	0.218	0.343	0.346	0.432	0.234	0.168	0.068	0.000	0.708	0.526	—

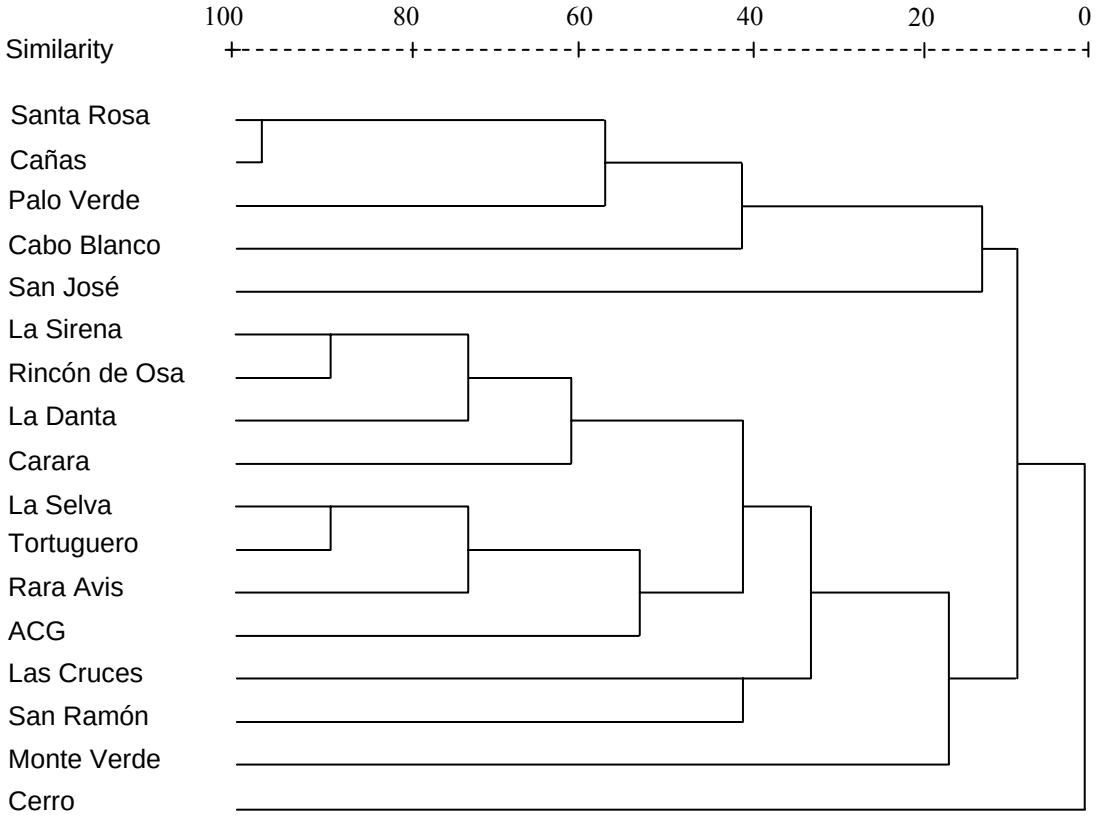

Figure 10 Reptile dendrogram based on Jaccard's Similarity Index values (percent) for 17 Costa Rican sites. Clustering is based on UPGMA method. Site abbreviations are Paso la Danta (La Danta); Área de Conservación Guanacaste (ACG); Cerro de la Muerte (Cerro).

with the dry forest sites and in the snake dendrogram, ACG, a LA site, did not cluster with the LA group, instead clustering with the LP-LA cluster.

Environmental Correlates

The reptile CCA also distributed the 17 localities along two primary gradients based on the environmental variables (Fig. 11). The first two axes explained 32.9% of the variance in the data. Axis one explained 18.9% of the variation and was negatively related to insolation and annual mean daily sunlight hours. Axis two explained an additional 14% of the variance and was positively correlated with elevation. Northwestern tropical dry forest sites were closest to each other (signifying they were more similar) as were LP and LA sites. Mid elevation sites were close to each other as well, and the high elevation site was distinct. Northwest dry forest sites were negatively associated with axis one, while Pacific and Atlantic lowland sites were positively related to axis1 and negatively related to axis two. Mid elevation sites were positively related to axes one and two, and Cerro de la Muerte was highly positively related to both axes.

Discussion

My analyses revealed three general patterns of herpetofaunal diversity in Costa Rica. First, alpha diversity was highest in lowland wet tropical forests on both the Pacific and Atlantic versants, and was lowest in the tropical dry forests and the highland site. Second, beta diversity was low within, and high between, ecoregions and elevations. Third, the CCA indicated that insolation, mean daily sunlight hours, and elevation were associated with the distribution of amphibian and reptile species, and therefore constrained patterns of species diversity. These findings suggest the species

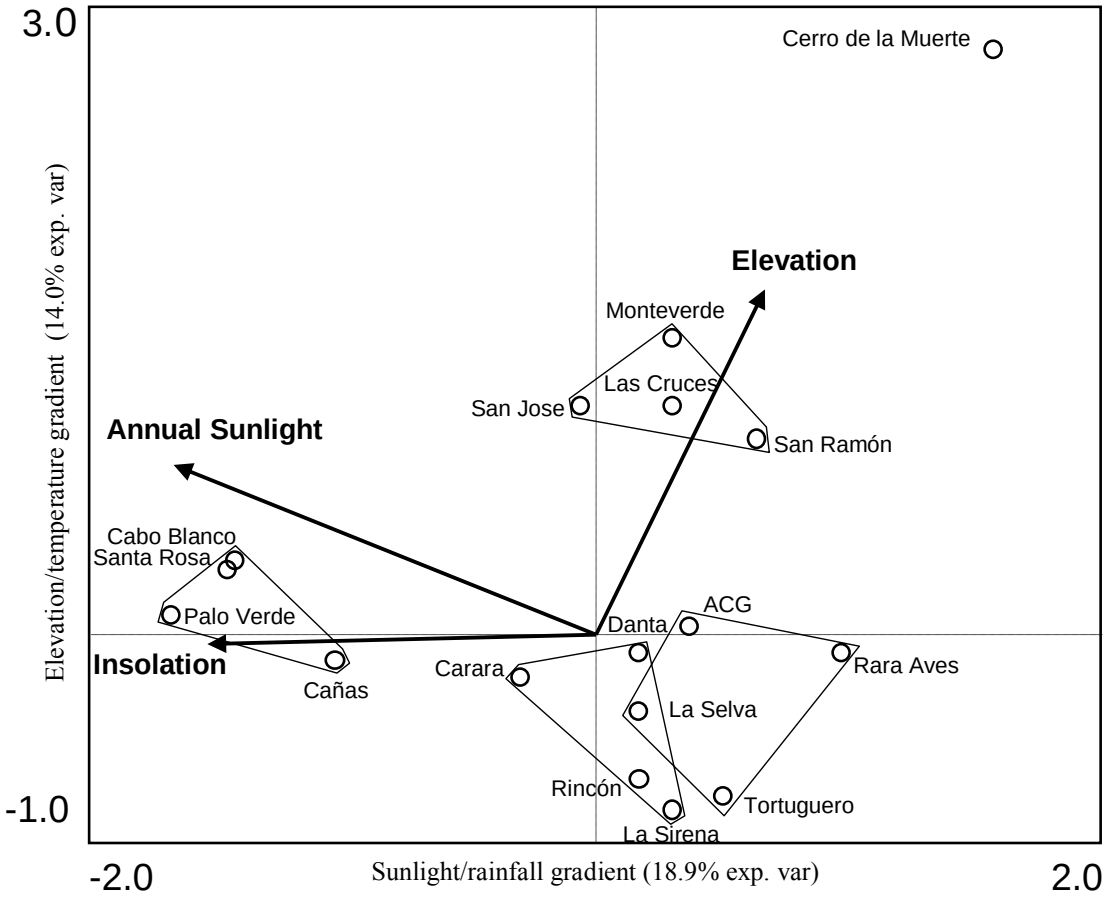

Figure 11. Results of reptile canonical correspondence analysis for 17 sites in Costa Rica. The relative importance of each environmental variable is indicated by the length of the arrow. Percentage of variation explained by each axis is provided in the parentheses. Abbreviations are as follows: Annual Mean Daily Sunlight Hours (Annual Sunlight); Área de Conservación Guanacaste (ACG); Paso de la Danta (Danta); Rincón de Osa (Rincón).

diversity patterns of both amphibians and reptiles were largely influenced by abiotic factors.

In both amphibians and reptiles, high and mid-elevation sites were separated along the elevation/temperature gradient, and lowland sites were spread along the sun/rain gradient. These results are not surprising given the physiology of amphibians and reptiles. For example, water requirements presumably exclude many amphibian clades (e.g., Caudata, Centrolenidae, Dendrobatidae) from TDF sites, resulting in overall lower alpha diversity of amphibians at TDF sites. Furthermore, the presence of amphibian species tolerant to hot dry conditions explains why TDF sites grouped towards the end of the sunlight gradient and clustered distantly from other sites in the amphibian analyses. Additionally, while reptiles are generally more resistant to desiccation, many have higher operating temperatures than amphibians, and several clades are heliophylic. These general biological characteristics help to explain why both the sun/rain gradient and the temperature/elevation gradient were important in determining reptile species diversity patterns.

Reptile species responded similarly to environmental cues at PL and AL sites, a pattern not seen for amphibians. Furthermore, beta diversity values were lower between the Atlantic and Pacific lowland rainforests for reptiles (especially snakes) than it was for amphibians. These differences were due to greater overlap of reptile species among groups of lowland sites that were separated by the Talamancan mountain range. Many of these species have ranges that include the AL and PL as well as adjoining areas in

Panama. In addition, a greater number of reptile species (especially snakes) are generalists and occurred on both versants, further decreasing beta diversity.

My results corroborate other studies of amphibian and reptile diversity in other regions. Previous work showed a combination of water and energy variables were important in shaping amphibian species richness patterns (Duellman, 1966; Rogers, 1976; Schall & Pianka, 1977; Owen, 1989; Crowe, 1990; Rodriguez *et al.*, 2005). Studies of reptile diversity also agree with our results, in that energy variables were important for determining species richness patterns at regional to continental scales (Schall & Pianka, 1977; Pianka & Schall, 1981; Rodriguez *et al.,* 2005).

Faunal Areas

According to Savage's (2002) herpetofaunal area designations, the 17 sites used in this study fall into these categories: 1) Lowland-Pacific Northwest (NW); Lowland-Southwest (SW); 2) Lowland-Atlantic (A); 3) Upland/Highland montane slopes and Cordillera Central (SCC); and 4) Highland-Cordillera de Talamanca (CT). My results largely agree with his classification, with some notable differences. For both amphibians and reptiles, lowland sites within each faunal area clustered together and were distinct from sites in other faunal areas. However, mid-elevation sites had relatively high beta diversity compared to the three groups of lowland sites and they did not cluster together (Figs 8 and 10). Interestingly, the grouping of species with abiotic variables in the CCA was similar among mid-elevation sites, even though beta diversity was relatively high among those sites compared to the low elevation sites (that also had similar CCA loadings) (Figs 9 and 11). The explanation for these results may reside in the region's

history. Savage (2002) postulated that high elevation species were compressed to lower altitudes during glacial maximums. This allowed for dispersal of mid and high elevation species between mountain masses. As populations moved higher in elevation during warming, speciation by vicariance could occur. This process was repeated during the cyclical cooling and warming cycles, generating distinct yet ecologically similar species on different mountains. This process would lead to the pattern of alpha and beta diversity that we described for mid elevation sites, with different suites of species at sites with similar environmental correlates.

Conservation Implications

My results have important conservation implications. The country's high regional diversity is a result of not only high alpha diversity values at local sites, but also high beta diversity values between them. This puts a premium on not only protecting sites with the highest alpha diversity values, but also a varied series of sites throughout the country that conserve differences in species among ecoregions. Fortunately, Costa Rica has done an excellent job of this as evidenced by the 17 sites used in this study. They range throughout the country, represent various assemblages and habitats and are all currently offered some level of protection. However, a new challenge to biodiversity arises with the increasing changes to the global climate (Houghton *et al.,* 2001). As alluded to by our work and Savage's (1966, 1982, 2002) historical biogeographical analyses, climate has played a paramount role in creating the pattern of species distributions across the landscape. Therefore, the risk to biodiversity lies in not only the outright extinction of species (Pounds *et al.,* 1999; Pounds *et al.,* 2006) but also in

distributional shifts and high species turnover at local communities. Climate change will cause remixing of species with unknown ecological consequences (Parmesan & Yohe, 2003; Root *et al.,* 2003; Peterson *et al.,* 2002). Studies such as ours enhance our understanding of the kinds of changes in diversity that may occur at local and regional scales, and should help facilitate informed conservation decisions in this changing world.

CHAPTER VII

CONCLUSIONS

This study adds to the understanding of species diversity patterns and the environmental factors related to these patterns. Our knowledge of species assemblages and distributions, often lacking in the Neotropics, was increased by the herpetofaunal surveys conducted at three sites in Costa Rica. Additionally, species diversity patterns and their causes at the regional level were explored using these surveys and other available species lists. Acknowledging the importance of historical factors and the extensive work conducted on those factors, this study took a bottom up approach in its analyses. By analyzing regional diversity in terms of alpha and beta diversity and then associating environmental variables to these patterns, I gained insight into non historical determinants of regional species diversity patterns.

The survey of Parque Nacional Carara, a transitional zone site on Costa Rica's central Pacific coast, gave evidence of a rich and unique herpetofaunal assemblage containing species from both the dry tropical forest to the north and the wet lowland rain forest to the south. Results illustrated that PNC's alpha diversity was higher than the dry forest site and lower than the wet forest site for both amphibians and reptiles. Furthermore, PNC shared roughly a quarter of amphibian and reptile species with the dry forest site and about half with the wet forest site. Carara was shown to be a transitional zone site falling neither in the northwest nor southwest herpetofaunal areas. Additionally, many species from both assemblages reach their range limit at or near the

park. As such, the park is important in the conservation of this unique herpetofaunal assemblage.

A survey of the eastern Área de Conservación Guanacaste showed a rich herpetofaunal diversity distributed among four sites. The diversity seen in these sites was different to that of the tropical dry forest found in the western ACG. Estación Caribe of the Rincón Rainforest was the most diverse site, even when accounting for sampling differences. This highlights the biodiversity value of the newly purchased Rincón Rainforest for the conservation area. The high elevation site, Estación Cacao, had the least similar assemblage and would benefit most from further survey work.

A survey of Reserva Natural Absoluta Cabo Blanco provided a preliminary list of amphibian and reptile species of the lower Nicoya Peninsula. It showed that the amphibian and reptile assemblage of RNACB was associated with that of the northwestern tropical dry forest. Alpha diversity of RNACB was lower than that of other dry forest sites, although lack of sampling along the Nicoya Peninsula made it difficult to assess why. The study also highlighted the importance of Laguna Balsitas to the local amphibian fauna. The lagoon served as the locus of amphibian life in the park.

Finally, a comparison of amphibian and reptile alpha and beta diversity among 17 sites throughout Costa Rica was conducted to discern patterns and explicate the relationship of abiotic factors to those patterns. These analyses showed highest alpha amphibian diversity in the lowland rainforests of the Pacific versant and highest reptile alpha diversity in lowland rainforests of the Atlantic versant. The analysis of beta diversity produced dendrograms showing lowland sites within three lowland ecoregions

(tropical dry forest, lowland Atlantic rain forest, lowland Pacific rainforest) being most similar. Mid elevation sites were less similar to each other and to other groups. The high elevation site was the most dissimilar. The analysis of environmental correlates showed two climate gradients, an elevation/temperature and a sun/rain, to be important in determining species diversity patterns for both amphibians and reptiles. The temperature/elevation gradient was important in separating high and mid elevation sites from lowland sites. A sun/rain gradient was most important in separating lowland sites by ecoregion (dry forest, Atlantic lowland rainforest, Pacific lowland rainforest).

This study showed that the current Costa Rican system of protected areas is effectively providing some form of protection for the overall diversity of amphibians and reptiles in Costa Rica. By protecting multiple sites in and among ecoregions, the network of protected areas is conserving both alpha and beta diversity and therefore the country's overall diversity of amphibians and reptiles. Highland sites can hold even further diversity. It is shown that even though alpha diversity of mid and high elevations may be lower that that of lowland sites, beta diversity between these site is very high, making them of great importance. More surveys are needed in the country's highland regions. This is especially true in the light of global climate change and global amphibian decline in highland regions. Further studies are also needed to assess the overall impact of global climate change on the country's herpetofauna.

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